DISCOVERY OF SEXUAL WING DIMORPHISM IN STAPHYLINIDAE (COLEOPTERA): *"OMALIUM"* *FLAVIDUM*, AND A DISCUSSION OF WING DIMORPHISM IN INSECTS

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Abstract.—Wing reduction and wing dimorphism in both sexes of an insect species are widespread phenomena. Sexual dimorphism in wing development is less common, and is previously unrecorded in the large beetle family Staphylinidae. *Omalium flavidum* Hamilton, a little-known forest staphylinid widespread in northeastern North America, has unusual wing dimorphism: flightless females and males, with minute vestigial wings and modifications often associated with wing loss; and fully-winged males, with distinctly elongate antennae, elytra, and legs. Occurrence of this and other patterns of sex-linked wing dimorphism in insects is reviewed and discussed. *Omalium flavidum* is redescribed and illustrated and a lectotype is designated for the species.

The presence of wings and the usually-associated ability to fly are conspicuous and fundamental features of most insects in the vast assemblage Pterygota. Nevertheless, secondary loss of wings in some descendants of winged insects has long been known (e.g., Wollaston, 1854, whose data were discussed by Darwin, 1859) and is quite widespread. In addition to orders whose members are universally wingless, strong wing reduction or loss has been recorded within all orders of insects except Odonata, Ephemeroptera, and Megaloptera (Roff, 1986a); although some Ephemeroptera have the hind wings vestigial or absent, they have not lost the ability to fly. Varying degrees of wing reduction have been recognized, which may be roughly categorized as: aptery, complete lack of wings; microptery, presence of very small wing vestiges (venation highly reduced or absent); and brachyptery, possession of distinctly shortened wings (venation almost normal to noticeably reduced, but apical region of wing strongly reduced). In fact, these are merely approximate points on a continuum of wing development, and additional terms have been proposed by some workers.

Most species are uniform with regard to wing development, but many show variation to different degrees. The occurrence of some kind of wing dimorphism (or polymorphism) within species is reasonably common in many orders of insects (Roff, 1986a and references therein; CSIRO, 1970). There are, however, different classes of dimorphism with respect to the distribution of morphs within the sexes, and some of these classes appear to be far more common than others (see Discussion and Table 4). The type of wing dimorphism reported here in *Omalium flavidum* Hamilton, namely micropterous females and both micropterous and macropterous males, appears to be extremely rare, as it has seldom been reported.

MATERIALS, METHODS, AND TERMINOLOGY

I examined a total of 161 specimens of *Omalium flavidum,* originating from or deposited in the following collections (acronyms as used in collection records, Appendix B):

AMNH   American Museum of Natural History, New York
ANMT   A. F. Newton, Jr. and M. K. Thayer collection, Chicago
CAS   California Academy of Sciences, San Francisco
CM   Carnegie Museum of Natural History, Pittsburgh
CNC   Canadian National Collection, Ottawa
CU   Cornell University, Ithaca, New York
FMNH   Field Museum of Natural History, Chicago
GHN   G. H. Nelson collection, Pomona, California
MCZ   Museum of Comparative Zoology, Cambridge, Massachusetts
UNH   University of New Hampshire, Durham, New Hampshire
USNM   National Museum of Natural History (Smithsonian Institution), Washington

Specimens were examined dry (point- or card-mounted), in alcohol, and KOH-cleared and slide-mounted. Drawings were made with a drawing tube on a Leitz Dialux 20 differential-interference contrast microscope; photomicrographs were taken on the Dialux with a Leitz Vario Orthomat 2 apparatus. Scanning electron microscopy was done with an AMRAY 1810; the specimens used were cleaned, critical-point dried, and gold-coated. Measurements, made with an ocular micrometer in a Leitz stereomicroscope, are defined as follows (all viewed perpendicular to line of measurement):

Antennal length: from constriction at base of scape to apex of last antennomere
Head length: along midline, clypeal apex to posterior ocellar margins, dorsal view
Head width: maximum width including eyes, dorsal view
Ocular length: maximum longitudinal distance, dorsal view
Interocular width: minimum distance between dorsal margins of eyes, dorsal view
Pronotal length: along midline, base to apex, dorsal view
Pronotal width: maximum width, dorsal view
Elytral length: longitudinal from front of humerus to elytral apex, dorsal view
Elytral width: maximum combined width of closed elytra, dorsal view
Hind tibial length: base to apex, not including apical spurs or setae
Hind tarsus, tarsomeres 1–4: base of tarsomere 1 to base of tarsomere 5
Hind tarsus, tarsomere 5: base to apex, not including claws
Metathoracic length: along midline, apex of mesosternal intercoxal process to apex of metasternum, ventral view
Metathoracic width: maximum width (at posterior margin), ventral view

Calculated figures in Tables 1 and 2 are:

Calculated length = Head length + Pronotal length + Elytral length
Eyes, 2 × width = Head width − Interocular width
Dorsal "area" (both eyes) = (Head width − Interocular width) × Ocular length

Statistical analyses (*t*-tests for pairwise differences between means, F_{max} tests for homogeneity of variances) were done using the computer program MYSTAT, a product of SYSTAT, Inc. Because of the disproportionately high number of winged males in the material available, some problems with condition of specimens, and receipt of some material very late in the project, not all specimens were measured. The map was produced using QUIKMap (ver. 2.5), a product of Axys Systems, Inc.

I did not attempt an exhaustive literature search regarding wing reduction or dimorphism/polymorphism in insects. Literature on Coleoptera was searched more thoroughly than that on other orders, and the paper is mainly focused on Coleoptera. In the Discussion, ordinal placement of non-Coleopteran families is indicated.

Some species include individuals with only slight reduction in wing length, which are probably capable of flight; these individuals are here lumped with fully-winged individuals as macropterous (=fully-winged), since they are functionally so. For simplicity, forms incapable of flight are likewise generally lumped together. For brevity, I will often refer to brachypterous or micropterous forms as −W and macropterous forms as +W. Likewise, for simplicity of expression, I will use the term wing dimorphism to encompass both dimorphism and polymorphism of wing development, since aptery, microptery, and brachyptery are functionally the same with respect to flight capability.

OMALIUM FLAVIDUM

Omalium flavidum Hamilton is a widespread (Fig. 1) but very poorly known eastern North American species of staphylinid beetle. It belongs to the mainly temperate subfamily Omaliinae, and more specifically to the tribe Omaliini. Its placement in Omaliini is supported by three derived characters (Thayer, in preparation): the presence of a (vestigial) seta-edged groove (Fig. 22) on the third abdominal tergite (Hammond, 1979, figs. 16, 17), a two-chambered sclerotized spermatheca in the female (Fig. 30), and the extremely reduced anterior tentorial arms. Females and micropterous males also have tarsi characteristic of Omaliini, with the basal four tarsomeres together shorter than the fifth (Hatch, 1957; Moore and Legner, 1979).

When Hamilton (1896:347) described *Omalium flavidum,* the genus *Omalium* was generally used in a much broader sense than now. There is no basis for placing the species in *Omalium* as now recognized (e.g., Lohse, 1964; Moore and Legner, 1979; Zanetti, 1987), since *O. flavidum* lacks the characteristic carinate mesosternum and aedeagal structure of that genus (abparameral surface of median lobe truncate well before apex; see Zanetti, 1987, figs. 45, 46, 47a–p). The head structure of *O. flavidum* is suggestive of the Palearctic genera *Carcinocephalus* and *Dialycera,* but I prefer not to change its generic placement or erect a new genus before completing a comprehensive study of the genera of Omaliini (Thayer, in preparation). Since the species was originally so incompletely described, I provide a more thorough redescription in Appendix A of the present paper.

Sexual and male dimorphism. Since this species was named and described very briefly almost 100 years ago (Hamilton, 1896), its only mention in the literature has been in catalogs. I have discovered that *O. flavidum* is a dramatically variable species, consisting of macropterous males (Figs. 4, 16a) and extremely micropterous females and males (Figs. 5, 16b). According to the conventions given above, *O. flavidum* (or
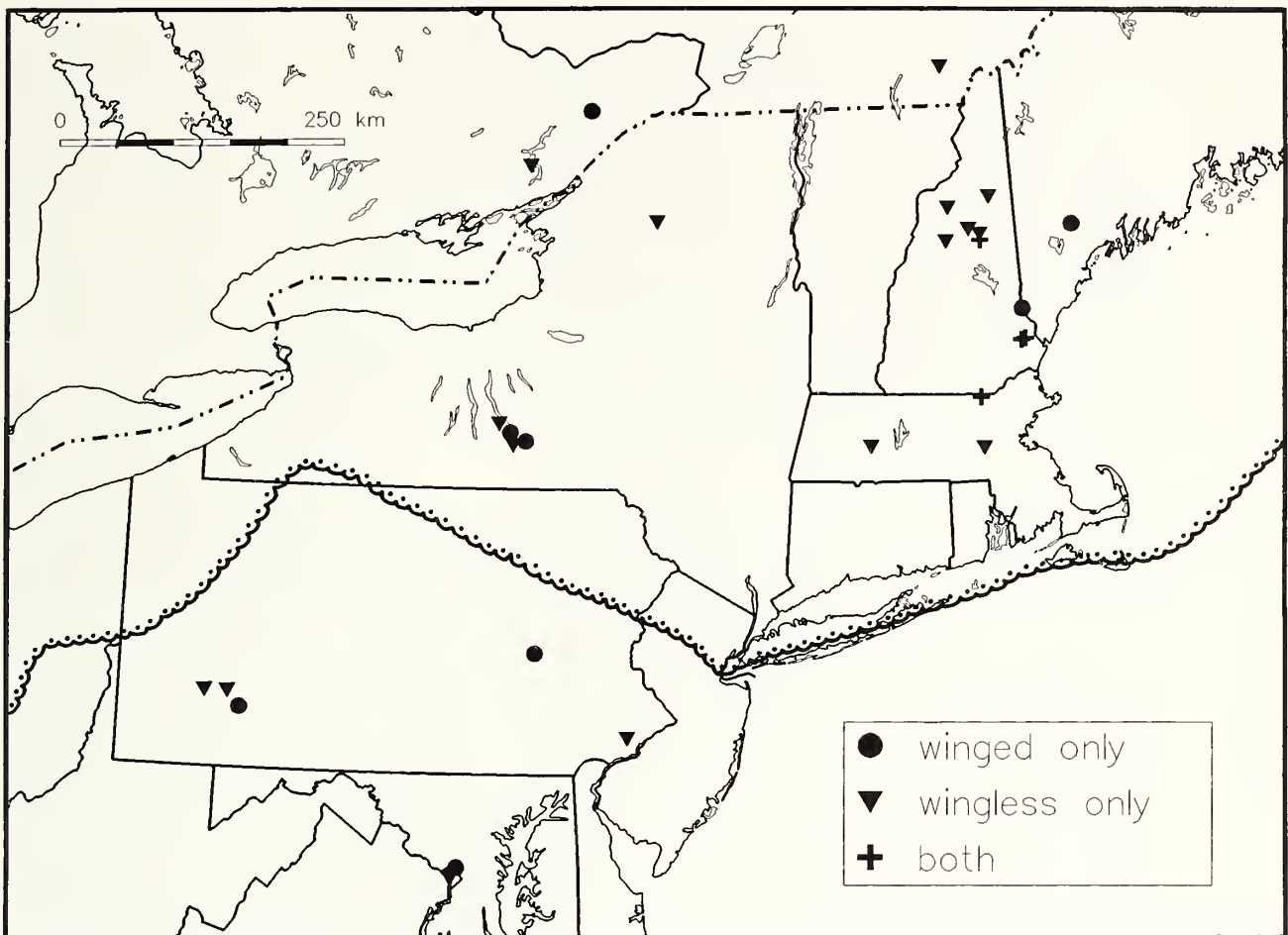
Fig. 1.   Northeastern U.S.A. and adjacent Canada, showing known distribution of *Omalium flavidum* Hamilton. Scalloped and dotted line shows approximate maximum limit of late Wisconsinan glaciation (after Morgan and Morgan, 1981).

the males collectively) can thus be called ±W. Micropterous (−W) individuals, including the syntype specimens, are all similar in appearance and readily distinguishable from the +W males (compare Figs. 4, 6, 8, 16a, 17, 23, with 5, 7, 9, 16b, 18, 24). Table 1 summarizes a number of features differentiating the morphs and Table 2 quantifies these and some other mensural characters.

Both wing morphs of *O. flavidum* differ from macropterous species of Omaliini in readily observable ways. The −W forms (♂ and ♀) have several modifications (derived features) often associated with wing loss: shortened elytra (common in −W Staphylinidae); reduced eyes, elytral humeri, and metathorax (Fig. 2a); strengthened elytral interlocking; loss of abdominal tergal wing-folding patches; and (♀ only) loss of the palisade fringe on tergite 7. The +W♂ differ from other macropterous Omaliini (and −W *O. flavidum*) in having: (1) filiform (instead of clavate) antennae, composed of slightly elongate antennomeres (Fig. 4); (2) elongate tarsi and tarsomeres (Figs. 2b, c, 17); and (3) very long elytra (Fig. 4). The first two of these resemble probably-primitive features for the subfamily, but appear to be secondarily derived within Omaliini; the third occurs sporadically within Omaliinae (presumably having evolved several times), but is unknown to me among other Omaliini.

Conspecificity of morphs. Despite these dramatic differences between +W and −W morphs, there are several morphological characters that argue for the different wing
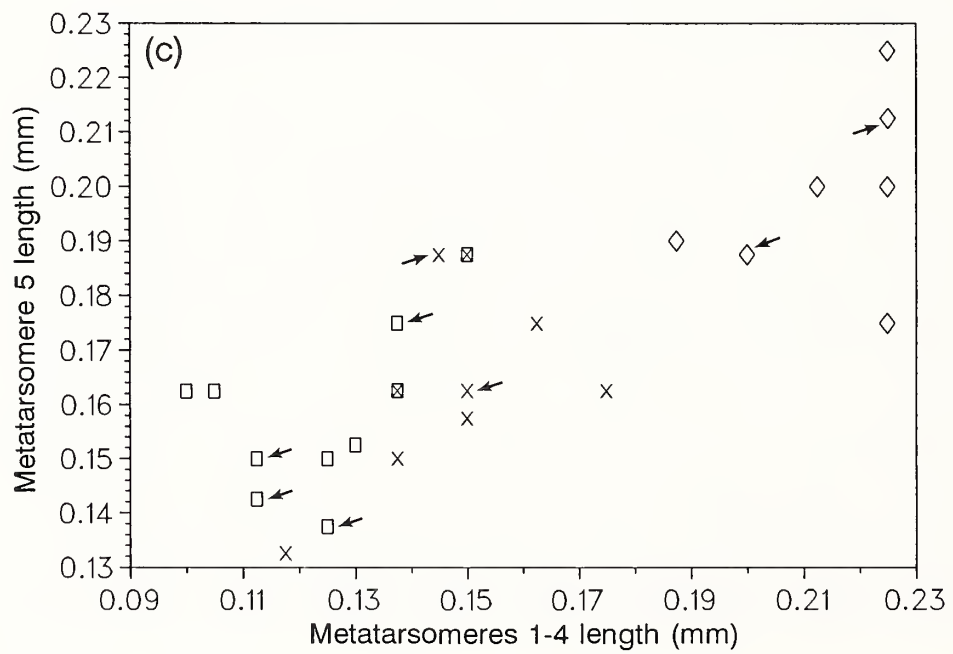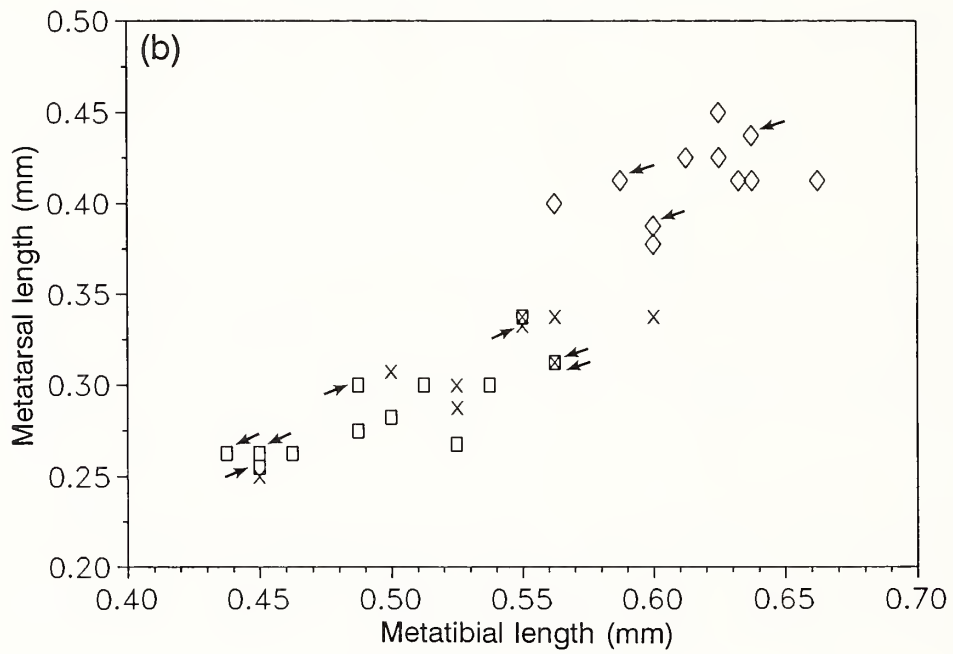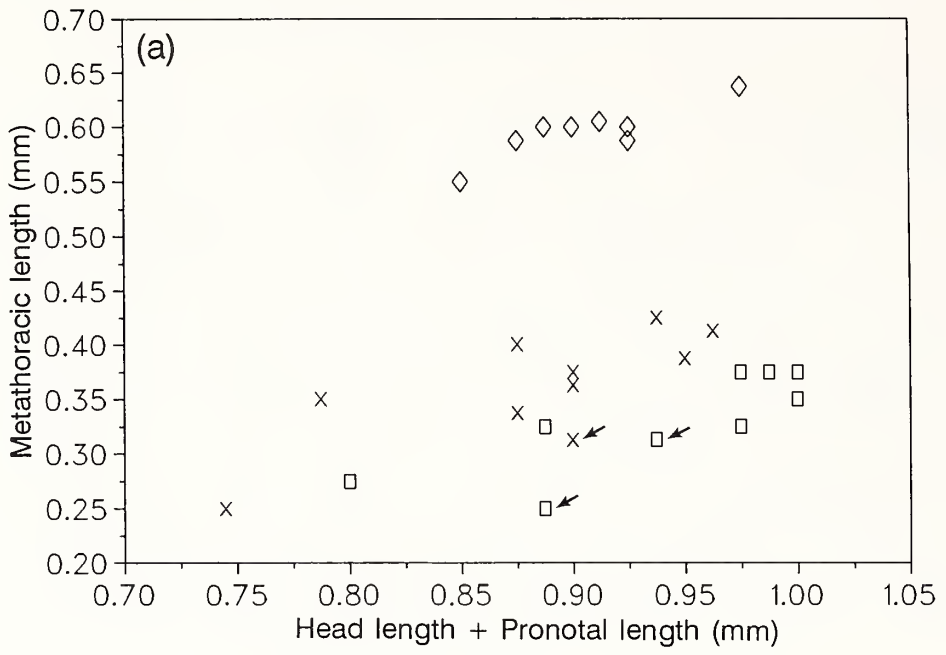
morphs being very closely related, and indeed conspecific. A feature unique to *O. flavidum* is the form of the empodial setae. Normally, Omaliinae (like most Staphylinidae) have a pair of subequal setae on each tarsal empodium. In some taxa one of the pair is lost, leaving the empodium unisetose (e.g., in the genus *Empelus*, related to Omaliinae, Thayer, 1987; Newton and Thayer, 1992); in others, for instance Corneolabiini (see Thayer, 1985), both are lost and the empodium is asetose. All morphs of *Omalium flavidum*, however, have one empodial seta greatly reduced in size and the other distinctly longer than usual (Fig. 19). I interpret this modification as a unique autapomorphy linking the morphs, although not necessarily indicating conspecificity. (*Carcinocephalus* (*Scribaia*) *blandus* (Luze) has unequal empodial setae, but the shorter one is much less reduced and the difference between the two is less.)

Male genitalia of Omaliinae, including Omaliini, usually provide characters diagnostic at the species level (Steel, 1957, 1960, 1964; Lohse, 1964; Smetana, 1981, 1985; Thayer, 1985; Zanetti, 1987; Watanabe, 1990), as in most Staphylinidae (and indeed most Coleoptera and many other Insecta). In several genera of Omaliini, there are also male secondary sexual characters of the abdominal sternites, hind tibiae, and/or hind coxae that differ between and serve to distinguish species (e.g., Steel, 1957; Zanetti, 1987; Watanabe, 1990; Thayer, in preparation). The aedeagi of the male morphs of *O. flavidum* (Fig. 28) are indistinguishable from each other in size, external morphology, and armature of the internal sac. In addition, the arrangement of setae at the apices of abdominal sternites 7 and 8 (Fig. 25) and the sclerotization pattern at the apex of sternite 8 (Fig. 25) are the same in both morphs and different from any I have seen in other Omaliinae. In addition, males of *O. flavidum* have dense long blunt sensilla on antennomeres 3–11; it is very unusual, if not unique among at least Omaliini, to have these sensilla located more basally than antennomere 6.

The pronotum of *O. flavidum* (females and both male morphs; Figs. 4, 5) is distinctive in having a raised median triangular area containing an impression on either side of the raised midline. This is unlike the pronotum of any other Omaliini known to me.

At least some genera of Omaliini show interspecific variation in the structure of the defensive gland associated with the anterior projection on abdominal sternite 8. These structures appear to be identical in females and the two male morphs of *O. flavidum* (Fig. 26). Similarly, the occurrence of apical membranous fringes (and their form, if present) and the distribution of apical spinules and ventral sensory structures (sensilla basiconica?) on the epipharynx varies among genera and, to some extent, species of Omaliinae. Females and both male morphs of *O. flavidum* all have the same epipharyngeal ornamentation (Fig. 14), which is distinguishable (albeit some-

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Fig. 2. *Omalium flavidum* Hamilton. (a) Metathoracic length vs. Head length + Pronotal length; (b) Metatarsal length vs. Metatibial length; (c) Length of metatarsomere 5 vs. combined length of metatarsomeres 1–4. ◇ +W♂, × −W♂, ☐ ♀. Arrows mark points representing specimens whose measurements are not included in Tables 1 and 2 because all their measurements could not be taken.
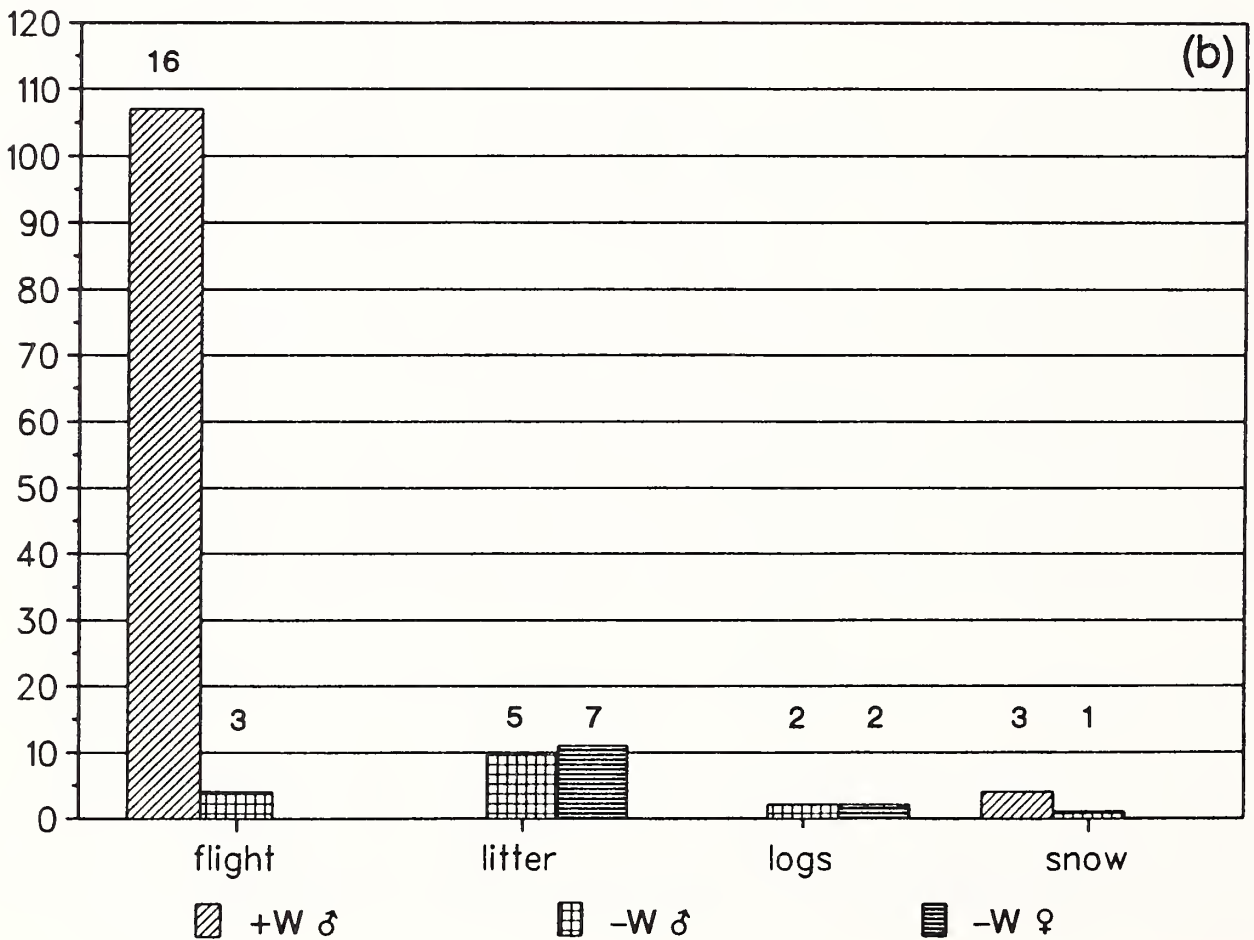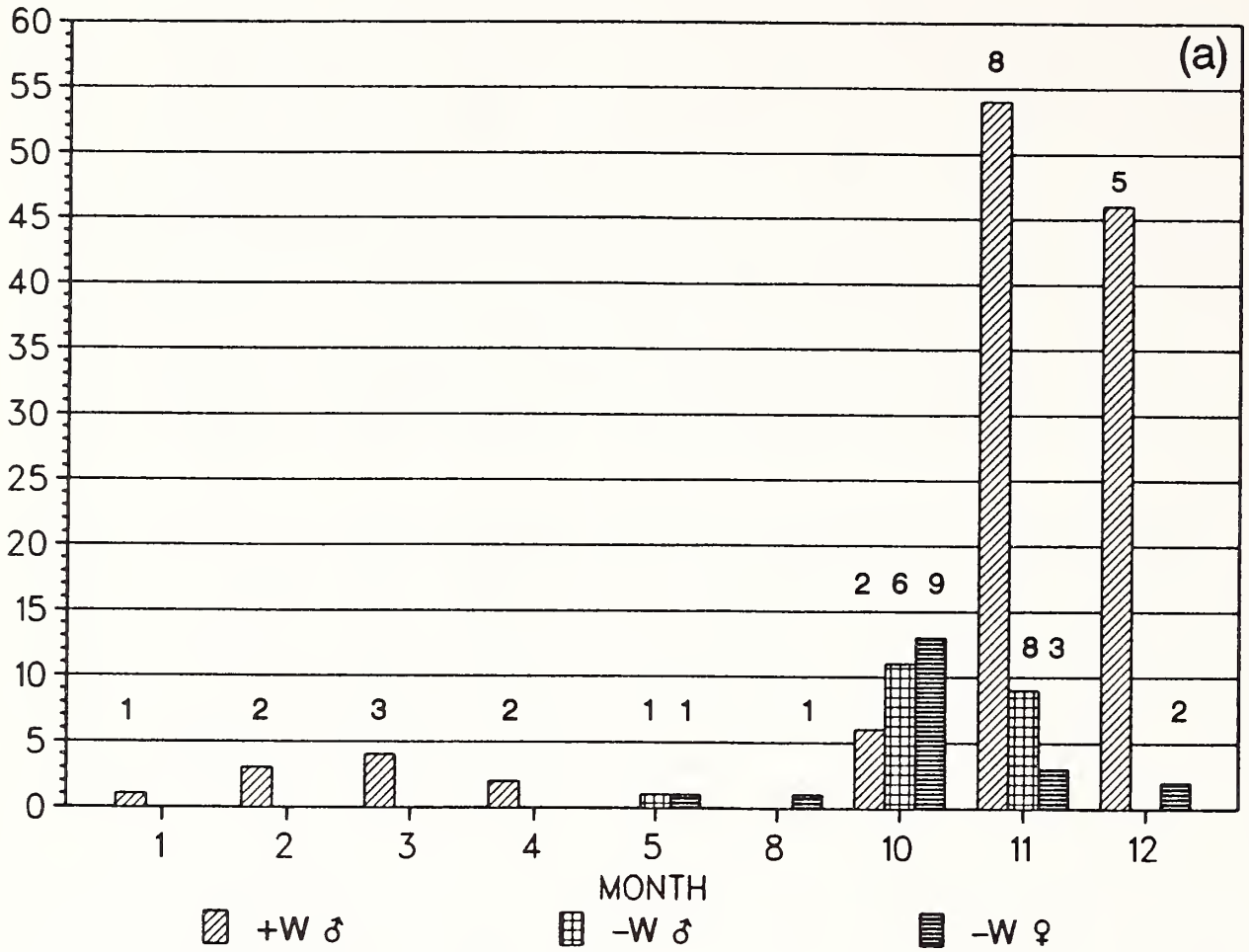
Table 1. Differences among wing morphs of *Omalium flavidum* (qualitative characters and means of some quantitative characters and ratios). See Table 2 for sample sizes, additional mensural characters, and standard deviations of measurements. All measurements are in mm.

Feature	♂ +W	♂ −W	♀ (−W)
Color	Dark brown (almost black) to reddish-brown	Reddish-brown; elytra lighter, abdomen darker	Head reddish-brown, rest yellowish- to reddish-brown
Antennae	Long (1.56)	Short (1.18)	Short (1.07)
Antennomeres	Elongate (Fig. 4)	Shorter (Fig. 5)	Shorter (cf. Fig. 5)
Eye size	Larger (Fig. 4)	Smaller (Fig. 5)	Smaller (cf. Fig. 5)
•Ocular length	0.17	0.12	0.12
•2 x Width	0.15	0.11	0.10
•Dorsal "area"	0.03mm²	0.01mm²	0.01mm²
Elytral length	1.47	0.78	0.80
Elytral humeri	Normal, prominent (Fig. 4)	Reduced (Fig. 5)	Reduced (cf. Fig. 5)
Elytral locking	Loose	Tightly interlocked with each other and scutellum (not fused)	Tightly interlocked with each other and scutellum (not fused)
Wings	Fully developed, ca. 4mm long (Fig. 16a)	Small stubs < 0.1mm long (Fig. 16b)	Small stubs < 0.1mm long (Fig. 16b)
Metathoracic length	Longer (Fig. 2a), 0.60	Shorter (Fig. 2a), 0.37	Shorter (Fig. 2a), 0.35
Hind tarsi	Longer (0.42), tarsomere 5 relatively short (Figs. 17, 2b-c)	Shorter (0.31), tarsomere 5 relatively long (Figs. 18, 2b-c)	Shorter (0.29), tarsomere 5 relatively long (Figs. 2b-c)
•Tarsal length/ Hind tibial length	0.67	0.58	0.56
•Tarsomere 5 length/ Tarsomeres 1-4 together	0.92	1.07	1.29
Basal abdominal spiracles (1-3)	Larger (Figs. 4, 6, 21)	Smaller (Figs. 5, 7, 22)	Larger (cf. Figs. 4, 6, 21)
•Spiracles 1-3 compared to 4	Distinctly larger	Slightly larger	Distinctly larger
Abdominal wing-folding patches	Present on tergites 4 and 5 (Fig. 23)	Absent (Fig. 24)	Absent
Tergite 7 palisade fringe	Present (Fig. 10)	Present (Figs. 11-12)	Absent

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Fig. 3. *Omalium flavidum* Hamilton. (a) Number of specimens of each morph seen, by month, with number above each bar indicating number of samples included; one collection of 2 −W ♀ in February not included; (b) Number of specimens of each morph seen, by generalized microhabitat, with number above each bar indicating number of samples included; "flight" includes intercept traps and "in flight."

Table 2. Mensural characters of wing morphs of *Omalium flavidum*. Mean ± standard deviation for indicated sample size (N) of each morph. Boldfaced entry indicates mean of that feature for that morph is significantly different (by t-test) from means of **both** other morphs at the P ≤ 0.001 level or at the higher (still P ≤ 0.05) probability level indicated. All features with means differing significantly between morphs had variances not differing significantly (P ≤ 0.05) among morphs, so the t-test is appropriate. Non-bold means with no P given are not significantly different from unmarked means of the other morphs at the P ≤ 0.05 level. Means of ratios are the means of individual ratios, not ratios of mean measurements. All measurements in mm.

Measurement or ratio	♂ +W	♂ −W	♀ (−W)
(N)	8	9	7
Calculated length	**2.38 ± 0.09**	1.66 ± 0.15	1.74 ± 0.14
Antennal length	**1.56 ± 0.10**	**1.18 ± 0.11** (P ≤ 0.045 vs. ♀)	**1.07 ± 0.08**
Head length	0.41 ± 0.02	0.39 ± 0.03	0.42 ± 0.04
Head width	0.53 ± 0.02	0.50 ± 0.04	0.54 ± 0.05
Ocular length	**0.17 ± 0.07**	0.12 ± 0.01	0.12 ± 0.01
Interocular width	0.38 ± 0.02	0.39 ± 0.04	**0.44 ± 0.03** (P ≤ 0.002 vs. +W♂) (P ≤ 0.011 vs. −W♂)
Pronotal length	0.50 ± 0.02	0.50 ± 0.05	0.53 ± 0.04
Pronotal width	0.61 ± 0.02 (P ≤ 0.019 vs. ♀)	0.62 ± 0.06	0.67 ± 0.05
Elytral length	**1.47 ± 0.06**	0.78 ± 0.09	0.80 ± 0.07
Elytral width	**0.97 ± 0.05**	0.77 ± 0.08	0.83 ± 0.07
Hind tibial length	**0.62 ± 0.03**	0.54 ± 0.04	0.51 ± 0.03
Hind tarsus, length tarsomeres 1-4 combined	**0.22 ± 0.02**	**0.15 ± 0.02** (P ≤ 0.003 vs. ♀)	**0.13 ± 0.02**
Hind tarsus, length tarsomere 5	**0.20 ± 0.02**	0.16 ± 0.02	0.16 ± 0.01
Metathoracic length	**0.60 ± 0.02**	0.37 ± 0.05	0.35 ± 0.04
Metathoracic width	**0.83 ± 0.05** (P ≤ 0.002 vs. ♀)	0.65 ± 0.05	0.70 ± 0.07

times subtly) from that of numerous other Omaliinae examined (Thayer, unpublished). Thus, characters on several parts of the body support the idea that the three forms discussed belong to a single dimorphic species.

Distribution and ecology. No additional collection records have been published since *O. flavidum* was described; the species is, in fact, distributed far more widely than just western Pennsylvania (type-locality "near St. Vincent"). As shown in Figure 1, *O. flavidum* occurs in the northeastern U.S. (District of Columbia and western Pennsylvania to Maine) and southeastern Canada (extreme southeastern Ontario and southern Québec). Relatively little habitat information is available for most collec-
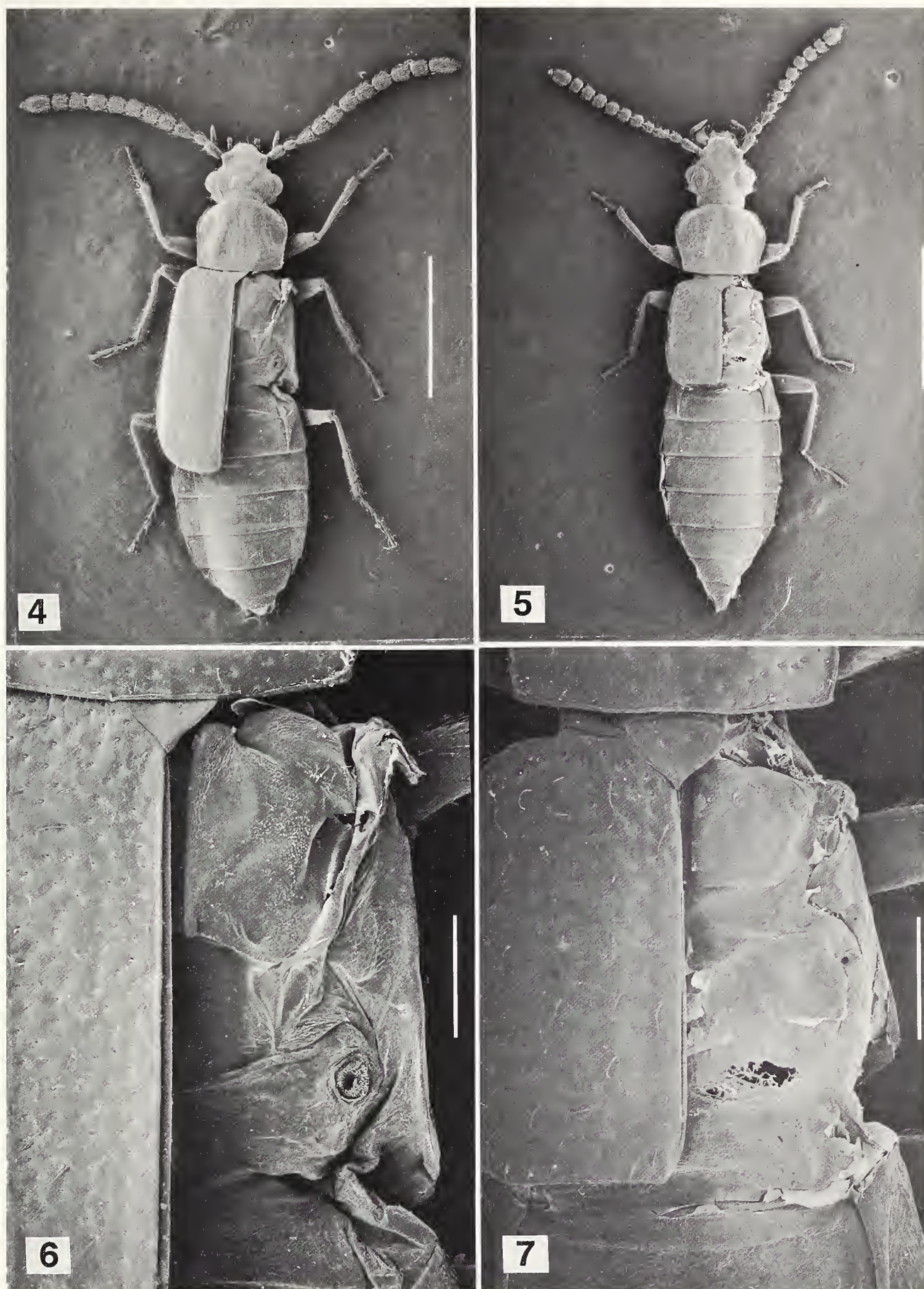
Figs. 4–7. *Omalium flavidum* Hamilton. 4. Habitus, dorsal view, right elytron and wing removed, +W♂. 5. Same, −W♂. 6. Detail of pterothorax, dorsal view, +W♂. 7. Same, −W♂. (Scale line: Figs. 4–5, 1 mm; Figs. 6–7, 200 μm.)

tions of *O. flavidum* (Appendix B), but it appears to be a forest-associated species. From explicit ecological data associated with some specimens and inference from locality and potential-vegetation data (Küchler, 1964) for others, it appears that *O. flavidum* occurs in Appalachian oak, northern hardwood, and northern hardwood-spruce-fir forests (classification according to Küchler, 1964). Its distribution in a densely (human-) populated and heavily-collected area makes it surprising that *O. flavidum* has been so seldom collected. The reason, as with some other Omaliinae (e.g., *Glypholoma rotundulum*, Thayer and Newton, 1979; *Omalorphanus aenigma*, Campbell and Chandler, 1987), appears to be its seasonality, presumably reflecting a preference for (or at least tolerance of) cool temperatures. Available records are concentrated in October through December, with activity (as indicated by trap catches) continuing through the winter (Fig. 3a). Only five collections of one individual each have been made from April through September (Fig. 3a), the more usual entomological collecting season in the area.

Of the 163 specimens examined (116 +W males, 23 −W males, 24 −W females), some ecological or microhabitat data are available for 141; these are plotted in generalized terms in Figure 3b. The relatively large number of +W males in flight intercept traps (mostly from four samples at three different sites; see Appendix B) indicates that they do fly, although the presence of two −W males in one sample and one each in two others suggests that the traps also acted as pitfall traps to a limited extent (see Chandler, 1987). Forest leaf and log litter are the only microhabitats from which *O. flavidum* has been collected, but the relatively low number of individuals thus collected (compared to flight intercept traps) and the absence of +W males in those collections raise the question of whether that is their real microhabitat. More investigation of the litter fauna in late autumn and winter could show them to be more abundant there than is now apparent; the species may occupy a more specialized microhabitat, such as mammal or bird nests. The few specimens cleared had no visible gut contents; the beetles are probably extra-orally digesting predators.

The available data show no obvious geographical pattern in the distribution of +W and −W males of *O. flavidum*. Both forms occur more or less throughout the species' range (Fig. 1) and both forms have been collected at four sites and three additional pairs of close sites. Eight sites are represented in collections by only +W males, 5 by only −W males, 7 by only females, 4 by only −W males and females, 2 by only males (+W and −W), and 2 by all forms.

Are there really no winged females? One must consider whether present collections accurately reflect the nature of the species or the lack of winged females is an artifact of relatively small sample size. A reasonable starting point in assessing this question is the null hypothesis that winged females of *O. flavidum* actually exist at the same within-sex frequency as winged males. (This is the case for, e.g., the omaliine *Glypholoma rotundulum*; see Discussion.) Testing this null hypothesis using all available data (listed in Appendix B) results in decisive rejection at the $P = 0.05$ level (Table 3, χ^2 and P columns, line 1). The large number of winged males from four flight intercept trap samples (and the mostly-fulfilled expectation that only winged specimens would be caught that way) may skew the result toward rejection of the null hypothesis by overestimating the real frequency of winged compared to wingless males. A more stringent test, therefore, can be made by reducing the influence of the flight intercept samples. This can be done in several ways; the χ^2 values and associated

Table 3. Chi-square tests of within-sex wing-morph frequencies of *O. flavidum* (using Yates' correction term for small expected numbers in one or more classes; see Sokal and Rohlf, 1969). Right column: maximum within-sex frequency of winged females (as a fraction of within-sex frequency of winged males) that does not require rejection of the null hypothesis that winged females exist.

	Null hypothesis: +W frequency in ♀ = +W frequency in ♂		Maximum +W♀ frequency as a fraction of +W♂ frequency
	χ^2	P	
1. # of specimens	115.08	<<<<0.001	0.20574
2. # of specimens except those from flight intercept traps	11.15	<0.001	0.49793
3. # of collections	23.41	<<0.001	0.36381
4. # of collections except flight intercept traps	9.34	<0.005	0.57527
5. # of specimens (flight intercept trap collections each counted as single specimen)	25.18	<<0.001	0.32279

probabilities are given in Table 3 (χ^2 and *P* columns), lines 2–5, for several possible treatments of the data. Even with these manipulations, the equal-frequency null hypothesis is overwhelmingly rejected at the $P = 0.05$ level.

An alternative class of null hypotheses can also be proposed: that winged females exist at a lower within-sex frequency than winged males. There are no obvious grounds for hypothesizing a particular ratio of female frequency to male frequency, but one can take an exploratory approach and calculate, under each method of counting the data (Table 3, lines 1–5), the highest frequency of winged females compared to winged males that could exist but be statistically indistinguishable ($P \geq 0.05$) from the observed values. These threshold frequencies are given in the right-most column of Table 3. Such statistical explorations show that the existence of winged females cannot be ruled out completely; if such females do exist, however, they occur at a distinctly lower frequency than winged males. Flight timing of conspecific males and females is often different, so there would not necessarily be a concurrent peak abundance of the hypothetical +W females. The series of samples from West Lebanon, Maine (see Appendix B) further supports the non-existence of +W♀, as trapping before and after the +W♂ peak produced a few +W♂, but no females.

DISCUSSION

Types and taxonomic distribution of dimorphism. Wing dimorphism (sensu lato) including flightless and flying morphs is the central concern of this paper, rather than monomorphic aptery, miccoptery, or brachyptery. Not all variably-winged taxa show the same pattern of dimorphism, however. Of seven possible intraspecific patterns of variation in wing development with respect to sex, two are relatively common; the others seem to be much rarer and one is as yet unknown. Table 4 summarizes the higher-taxon placements of wing-dimorphic species reported in the literature, categorized by the wing condition in each sex. One of the two most common types

Table 4. Distribution of wing-dimorphisms with respect to sex; each taxon shown includes at least 1 species with the type of dimorphism indicated.

	+W♂
+W♀	MONOMORPHICALLY +W SPECIES: Most members of most orders of pterygote insects
±W♀	Homoptera: Aphididae [2,7] Hemiptera: Miridae [6] Hymenoptera: Bethylidae, Formicidae [2] Lepidoptera: Arctiidae, Geometridae, Lymantriidae, Pyralidae [8] Diptera: Sciaridae, Tipulidae [5]
−W♀	Embioptera [32] Phasmatodea: Phasmatidae [2] Orthoptera: Tettigoniidae [2] Blattodea: Blaberidae [2] Mantodea: Amorphoscelidae, Mantidae [2] Psocoptera [2] Homoptera: Coccoidea [2] Hemiptera: Microphysidae, Miridae [6] Strepsiptera [2] Coleoptera: Cerambycidae, Dascillidae, Elateridae, Lucanidae, Phengodidae (as Cantharidae), Scarabaeidae [31] 　　Corylophidae, Drilidae, Lagriidae, Lampyridae, Meloidae, Ptinidae [17] 　　Rhipiphoridae [2] Hymenoptera: Bethylidae, Cleptidae, Diapriidae, Dryinidae, Mutillidae, Sclerogibbidae [2] Lepidoptera: Arctiidae (s. 1.), Gelechiidae, Geometridae, Hepialidae, Lasiocampidae, Lymantriidae, Megalopygidae, Momphidae, Noctuidae, Oecophoridae, Olethreutidae, Psychidae (and related families), Pyralidae, Symmocidae, Syntomidae, Tortricidae [8] Diptera: Cecidomyiidae, Chironomidae, Phoridae, Sciaridae, Tipulidae (some as Limoniidae) [5]

References: [1] Crowson (1981);   [2] CSIRO (1970);   [3] Kalmus (1945) (Agaonidae as Chalcididae);   [4] Venturi (1964);   [5] Hackman (1964);   [6] Southwood & Leston (1959);   [7] Hille Ris Lambers (1966);   [8] Hackman (1966); [9] Darlington (1936);   [10] Darlington (1943);   [11] Lindroth (1979);   [12] Den Boer *et al.* (1980);   [13] Langor & Larson (1984);   [14] Liebherr & Hajek (1986);   [15] Desender (1989);   [16] Shute (1980);   [17] Jackson (1928); [18] Pope (1977);   [19] Hammond (1985);   [20] Paulian (1988);   [21] Dybas (1978);   [22] Taylor (1978; 1981);

Table 4 (continued). "–W" includes brachypterous, micropterous, and apterous. Numbers [x] indicate sources listed below; see Literature Cited for full references.

±W♂	–W♂

No examples found	Psocoptera [2]
	Thysanoptera [3]
	Coleoptera: Scolytidae [1]
	Hymenoptera:
	   Agaonidae [2,3]
	   Torymidae [2]
	Diptera: Sciaridae [4]
	   Tipulidae (as
	   Limoniidae) [5]

Orthoptera: Acrididae [2]
   Gryllidae, Pyrgomorphidae [26]
Blattodea: Blaberidae [2]
Isoptera [2]
Zoraptera [2]
Homoptera: Aphididae [2]
   Delphacidae [29]
Hemiptera: Aradidae, Berytidae, Cimicidae, Dipsocoridae, Hebridae,
   Hydrometridae, Mesoveliidae, Miridae, Nabidae, Pyrrhocoridae, Reduviidae,
   Rhopalidae, Saldidae, Tingidae, Veliidae [6]
   Gerridae [6,27]
   Lygaeidae [6,28]
Thysanoptera [3]
Coleoptera: Carabidae [9-15]
   Chrysomelidae [16]
   Cicindelidae, Curculionidae, Endomychidae, Hydrophilidae, Nitidulidae [17]
   Coccinellidae [18,19]
   Dermestidae [9]
   Dryopidae [20]
   Ptiliidae [21,22]
   Staphylinidae [19,23,24,this paper]
   Trogidae [25]
Lepidoptera: Elachistidae, Gelechiidae, Noctuidae, Tineidae, Tortricidae,
   Yponomeutidae (as Hyponomeuthidae) [8]
Diptera: Chloropidae, Sphaeroceridae (as Borboridae), Tipulidae [5]
   Sciaridae [30]
	Psocoptera [3]
	Homoptera: Adelgidae,
	   Pemphigidae [2]
	Thysanoptera [3]
	Diptera: Cecidomyiidae [5]

Embioptera [32]
Homoptera: Aphididae [7]
Coleoptera: Carabidae? [33]
   Dermestidae [34]
   Staphylinidae [this paper]
Diptera: Sciaridae [5,35]
   Tipulidae (as Limoniidae) [5]
	MONOMORPHICALLY
	–W SPECIES:
	Some members of most
	orders of neopterous insects

[23] Hammond (1979); [24] Campbell (1983); [25] Scholtz (1981); [26] Harrison (1980); [27] Vepsäläinen (1978); [28] Slater (1975; 1977); [29] Denno & Grissell (1979); [30] Steffan (1973; 1975); [31] Van Dyke (1933); [32] Ross (1970); [33] Liebherr (1989): *Tanystoma diabolica* may be ±W♂/–W♀; it was described from only 5 specimens (2 +W♂, 1 –W♂, 2 –W♀); [34] Barber (1947; 1948); [35] Steffan (1966).

is that in which both sexes show similar variation in wing development ($\pm$W♂/$\pm$W♀), although morph frequencies may differ between the sexes. Such non-sexual dimorphism has been recorded in some members of at least 49 families in ten orders (Table 4). Among these, Isoptera are a highly specialized case, with macropterous reproductives and apterous soldier and (in higher termites) worker castes occurring in both sexes.

The other commonest pattern of intraspecific wing variation is +W♂/−W♀, one of the six types involving sexual dimorphism. This pattern occurs in all Strepsiptera (CSIRO, 1970), most Embioptera (Ross, 1970), and in some members of at least 49 families in 11 other orders.

Other sex-related patterns of wing variation appear to be distinctly rarer than these two, especially among Coleoptera. The pattern of +W♂/$\pm$W♀ has been reported in at least ten families in five orders (Table 4). Most species of Formicidae (Hymenoptera) can be regarded as a special case of this category, having two or more female castes (+W reproductives, −W workers and sometimes soldiers) and only +W males. Aphididae (Homoptera) (Hille Ris Lambers, 1966) and Lymantriidae and Pyralidae (both Lepidoptera) show seasonal (generation-to-generation) rather than simultaneous (within-generation) dimorphism (Hackman, 1966).

I found no reports of species that are $\pm$W♂/+W♀, and only a few (in four orders) that are −W♂/$\pm$W♀. Species with the pattern −W♂/+W♀, in at least seven families in five orders, include Agaonidae (Hymenoptera) (Kalmus, 1945, as Chalcididae; CSIRO, 1970) and some of the Torymidae (Hymenoptera) that parasitize them (CSIRO, 1970).

The pattern of primary interest in this paper is the also rare one of $\pm$W♂/−W♀. This pattern has been reported previously in four orders (see Table 4), mostly in a single species per family. Discovery of this pattern in *Omalium flavidum* Hamilton provides the first case of this (and in fact any) pattern of sexual wing dimorphism in Staphylinidae.

Associated morphological changes. Various morphological changes beyond lack of wings are commonly associated with the evolution of flightlessness in insects. Coleoptera, with their front wings modified into elytra and related specializations of thoracic structure, have diverged significantly from other insects in general body organization. Many modifications accompanying wing loss in Coleoptera thus have no close parallel in other orders, and the following discussion deals principally with Coleoptera.

The most extreme modifications are generally found in monomorphically brachypterous species, particularly those belonging to entirely flightless lineages. In the latter cases flight capability presumably was lost in a temporally rather distant ancestor of any extant species, allowing more time for development of other modifications than would be expected for a wingless species having all fully-winged relatives. At its fullest development (short of reduction to a larviform morph), what could be called a "flightless beetle syndrome" includes: loss of wings and flight muscles (direct and indirect); rounding of elytral humeri; tighter than normal locking, or even fusion (ankylosis), of the elytra to each other; reduction in length and width of the metathorax; reduction in elytral length (sometimes to tiny vestiges); loss of abdominal wing-folding and wing-toiletry devices (Hammond, 1979, 1985); reduction in dorsal sclerotization of the pterothorax and (except in brachelytrous forms, e.g., Staphylin-

idae and Meloidae: *Meloe*) abdomen; reduction in size of spiracles of abdominal segment 1 (Rüschkamp, 1927; Jackson, 1956); loss of eyes; and sometimes (depending at least partly on microhabitat) reduction in antennal length and/or body pigmentation. Within a number of insect orders, ocelli are sometimes reduced or lost along with wings (Kalmus, 1945). Very atypically for Coleoptera, most Omaliinae (Staphylinidae) have ocelli, but no correlation of wing and ocellar loss has yet been found in this group.

Jackson (1928) found no external differences between macropterous and brachypterous individuals of *Sitona hispidula* (Curculionidae). The brachypterous morphs of many other wing-dimorphic species of Coleoptera (also Lygaeidae [Hemiptera]; Slater, 1977) do, however, exhibit some features of the "flightless beetle syndrome" despite normal development of the corresponding features in macropterous conspecifics. A few examples from Coleoptera follow. Reduction of eyes in wingless morphs, reported here in *O. flavidum,* has also been reported in *Aglyptinus dimorphicus* (Leiodidae, Peck, 1978), *Leistus americanus* (Carabidae, Darlington, 1936), and species of the genus *Ptinellodes* (Ptiliidae, Dybas, 1978). The last-named also show reduction of elytra in the wingless morph ("vestigial morph" of Dybas, 1978), as do *Platystethus nitens* (Staphylinidae, Hammond, 1985) and *Omalium flavidum* (reported here). Reduction of the elytral humeri occurs in wingless morphs of *Trox* spp. (Trogidae, Scholtz, 1981), *Pseudomacronychus* spp. (Dryopidae, Paulian, 1988), *O. flavidum,* and rarely in dimorphic Carabidae (though commonly in monomorphically −W species; Darlington, 1936). Reduction in metathoracic size has been found in wingless morphs of *Platystethus nitens* (Staphylinidae, Hammond, 1985) and *Tanystoma maculicolle* (Carabidae, Liebherr and Hajek, 1986) as well as *O. flavidum,* while reduction in dorsal meso- and metathoracic sclerotization occurs in *Sitona hispidula* (without reduction in size; Curculionidae, Jackson, 1928) as well as *O. flavidum.* Reduction in size of the spiracles of abdominal tergite 1 seems not to have been reported previously in dimorphic beetle species, but occurs in −W males of *O. flavidum.*

Discussion of the state of flight muscles is seldom part of normal taxonomic work, but in special studies of the subject, reduction or loss of these muscles in wingless and some winged individuals has been found in *Sitona hispidula* (Curculionidae, Jackson, 1928), *Bembidion lampros* (Carabidae, Langor and Larson, 1984), and several other species of Carabidae (Den Boer et al., 1980). In many cases (including some monomorphically macropterous species discussed by Den Boer et al., 1980), there is seasonal change in development of flight muscles in individuals. Undoubtedly more such examples will be found when more species are investigated in this regard. Fusion of elytra seems not to have been recorded in dimorphic Coleoptera, although Lindroth (1949) mentioned two species of Carabidae in which some brachypterous individuals show a slight amount of fusion.

Two features of the "flightless beetle syndrome" that are quite rare in wingless morphs of dimorphic species are loss of abdominal wing-folding patches and loss of "palisade" or "wing-toiletry" fringes (Hammond, 1979). Hammond (1985) surveyed over 300 species of wing-dimorphic beetles in several families and found (in addition to *Ptinellodes* spp., Dybas, 1978) only one, *Rhyzobius litura* (Coccinellidae), dimorphic in presence of wing-folding patches and only *R. litura* and some species of *Othius* and *Mycetoporus* (both Staphylinidae) dimorphic in presence of the palisade fringe.

Glypholoma rotundulum (Staphylinidae: Omaliinae) is dimorphic in the size, not presence, of its wing-folding patches (Thayer, unpublished). *Omalium flavidum*, as reported here, provides an additional example of dimorphism in each of these features (see above and Appendix A), although the distributions of the reductions are not concordant. This non-concordance runs counter to the sometimes-observed pattern of morphological changes associated with wing loss apparently evolving in a certain sequence (at least within a given lineage), yielding a nested pattern of losses (Jeannel, 1926; Hammond, 1979; Scholtz, 1981).

Mechanisms producing and maintaining wing dimorphism. Roff (1986a, b) reviewed mechanisms of wing length determination; the number of species whose wing-determination has been studied in detail is still extremely small. At least many cases of wing dimorphism are what Clark (1976) called "genetically determined polymorphism" (Roff [1986a, b] and Roff and Fairbairn [1991] cited a total of 29 examples). Sequential wing dimorphism (e.g., seasonal changes in many aphids: Hille Ris Lambers, 1966; Lees, 1966; Clark, 1976; MacKay et al., 1983) and some cases of non-seasonal dimorphism appear, on the other hand, to be largely what Clark termed "environmentally cued polymorphism," in which environmental factors interact with the genotype to produce different morphs under different conditions. Such a mechanism was suggested by Dybas (1978) for some Ptiliidae and by Denno and Grissell (1979) for a species of Delphacidae (Homoptera). There can also be genetic variation in presence or thresholds of environmental response (Vepsäläinen, 1978; Denno and Grissell, 1979). Morph determination in individuals is probably hormonally mediated, possibly by levels of juvenile hormone (Southwood, 1961; Wigglesworth, 1961; Roff, 1986a, b).

Even where genetic control of wing morphs occurs, there appears to be variation in its nature. In the 29 examples cited by Roff and Fairbairn (1991) and Roff (1986a, b), single-locus systems are more common in holometabolous orders and polygenic systems far more common in paurometabolous orders. Roff (1986b) argued that even if wing dimorphism arose in a species as a single-locus mutation, selection would favor replacement of single-locus control by a system of polygenic control because of the greater flexibility of polygenic systems in responding to environmental fluctuations. Roff (1990a) and Roff and Fairbairn (1991) gave evidence for the occurrence of antagonistic pleiotropy in maintenance of wing dimorphism in *Gryllus firmus* (Orthoptera) (and potentially in other species) in the form of a tradeoff between migration ability and earlier age at reproduction. The contention in the former work, however, that "expression of wing form . . . in . . . wing dimorphic insects in general, is highly dependent on environmental conditions such as temperature and photoperiod . . ." appears to be based almost entirely on paurometabolous insects (e.g., Honek, 1976, 42 paurometabolous, 5 holometabolous species). Roff and Fairbairn (1991), in contrast, said ". . . the available evidence suggests a genetic basis [for wing dimorphism] in most species. . . ." The seeming difference between holometabolous and paurometabolous insects in the type of genetic control of wing polymorphism and the still-limited data bearing on the question leave the importance of environmental conditions to morph determination in Holometabola uncertain.

I have found no explicit discussions of the genetic or non-genetic basis of sexually dimorphic wing development; Roff (1986a) listed two species of Aphididae (Homoptera) as having polygenic wing morph determination, but did not specifically

discuss sexual wing dimorphism. Work done on sexual dimorphism of wing development in aphids (e.g., Lees, 1966; MacKay et al., 1983) suggests that determination of morphs in female aphids is under complex environmental control. Determination of wing morphs in male aphids has been studied far less, and it is not clear whether it is produced by genetic or environmental factors (or both). In any case, the extreme complexity of aphid life cycles leaves some question as to how applicable the aphid results are to other insects.

Ecology and evolution of wing loss. On the basis of observed occurrences and theoretical considerations, various workers have summarized or predicted conditions under which brachyptery is favored, including: small-area stable ("permanent") habitats (Darlington, 1943; Vepsäläinen, 1978), including those on mountains (Darlington, 1943; Scholtz, 1981); isolated habitats (in combination with stability and areal limitation; Lindroth, 1949; Vepsäläinen, 1978); cold areas or seasons of activity (Downes, 1965; Byers, 1969); caves (Jeannel, 1926; for different reasons, Barr, 1968); and areas providing distinctly suboptimal conditions for a species (Jeannel, 1926, but with little or no support from other workers). It is also well known that many nidicolous or parasitic insects are wingless (e.g., Arixeniina and Hemimerina [Dermaptera]; Phthiraptera [loss of wings probably preceded parasitism; Lyal, 1985]; Cimicidae and Polyctenidae [Hemiptera]; Staphylinidae: Amblyopinini and Leiodidae: Platypsyllinae [Coleoptera]; Siphonaptera; Nycteribiidae, Hippoboscidae, and Streblidae [Diptera]). Hackman (1964) attributed most cases of wing loss in Diptera (aside from halobionts and parasites) to the adults' living in "concealed terricolous habitats" (including galleries of social insects), where he suggested selection might favor morphological changes improving the ability to run, even at the expense of the ability to fly. The unusual groundplan of Coleoptera, with the flight wings protected by elytra, facilitates the coexistence of good running and flying abilities and presumably would reduce selective pressure against flight in microhabitats with restricted passageways. Wing loss does appear to be less common in litter-dwelling Coleoptera than Diptera, although soil-inhabiting beetles are more likely to be wingless (e.g., Coiffait, 1960).

Roff (1990b) judged available data to be consistent with the idea of habitat stability favoring evolution of flightlessness, but not yet adequate to test the importance of other potential factors such as temperature or physical constraints. Barbosa et al. (1989) argued convincingly that habitat stability alone may not be a sufficient explanation for evolution of brachyptery or wing dimorphism; the way in which a species interacts with its habitat may also play a key role.

In contrast to the idea of strongly directional selection for brachyptery in stable environments, Hamilton and May (1977) demonstrated that even in relatively unchanging habitats an evolutionarily stable strategy (ESS) is likely to include a significant probability of migration of offspring from the parent's "unitary site" (individual site occupied by one indivdual in the model). Although these authors mentioned the relevance of their models to insect species having flying males and flightless or flight-dimorphic females, they did not discuss the key relationship between unitary site size and capability of dispersal by means other than flight. How large is an insect's unitary site? In a species whose individuals can move beyond their natal unitary site by walking, swimming, or larval ballooning (Barbosa et al., 1989), even complete loss of flight capability would not preclude an ESS involving significant probability

of dispersal. This potential nonidentity of flight capability and dispersal/migration ability, admittedly difficult to investigate, is often overlooked in discussions of wing and flight loss.

Reasons for the origin, persistence, and spread of wing loss remain somewhat uncertain and may well vary among species. Although Jeannel suggested "senility" of lineages (1926) or inheritance of changes caused directly by effects of cave environments (1943), there seems little reason to doubt that random mutations are the underlying cause of wing loss. Darlington (1936) suggested that wing atrophy arises through spontaneous mutations (occurring persistently at a significant rate), and might in some cases increase through simple accumulation of the mutations in the absence of natural selection against wing loss. On the other hand, it seems likely that natural selection could often be involved, whenever advantages of winglessness (or flightlessness) outweigh selective pressures favoring flight. Both flight and the synthesis of muscle and other tissues needed for it are energetically expensive (Roff and Fairbairn, 1991 and references therein). Wingless forms, by rechanneling this biosynthetic and locomotory energy into earlier or greater total reproduction, might gain a substantial fitness advantage over +W forms under circumstances where flight was not essential (Darlington, 1936, 1943; Byers, 1969; Dybas, 1978; Roff and Fairbairn, 1991; but not Taylor, 1978). (Evidence for such an "energy conservation hypothesis" in bacterial systems is mixed [Zamenhof and Eichhorn, 1967; Dykhuizen, 1978].) In contrast, Regal's (1977) "noise suppression theory" proposes that natural selection favors loss of non-essential structures because such elimination removes informational noise (thus potential errors) from the process of transcription of the genome.

Wing dimorphism has been predicted to occur when the habitat (or microhabitat) of a species is mostly stable with occasional disruptions (Darlington, 1936; Southwood, 1962; Hammond, 1985; Roff, 1986a). When a species has different habitat requirements at different times of year, the selective advantage of dispersing may vary seasonally (Cohen, 1967); under such conditions, sequential wing dimorphism may be favored in bi- or multivoltine species (Harrison, 1980). Some authors (e.g., Lindroth, 1949; Den Boer et al., 1980; Roff and Fairbairn, 1991) have regarded wing dimorphism or polymorphism as an intermediate state in the transition to brachyptery, in essence predicting that dimorphic species should be found in the same situations as monomorphically brachypterous ones, but in habitat patches that have been stable a shorter time than those with brachypterous species.

There has been relatively little discussion of possible reasons for sex-biased wing dimorphism. Downes (1965) and Byers (1969) suggested that in the Arctic the severe energetic demands of the climate have caused selection for a $+W\delta/-W♀$ pattern. The short available reproductive season there makes it advantageous for females to produce their eggs as soon as possible after emerging in the spring; the resulting extra weight of mature eggs would make female flight energetically very expensive, perhaps impossible. In a number of arctic species, therefore, females appear to have maximized their reproductive effort by abandoning flight ability and males have specialized in mate location and dispersal by flight, the latter permitting outcrossing. (Some other arctic species have instead abandoned outcrossing or even mating.) Such arguments may apply equally well to cold montane areas at lower latitudes.

Other circumstances associated with the pattern of $+W\delta/-W♀$ are: (1) in some

Hymenoptera, adaptations for burrowing (or host-seeking behavior in other tight places) by females and transport of therefore −W females by males (CSIRO, 1970) and (2) in some eastern North American forest Lepidoptera, a complex of life-history traits including polyphagy on dominant trees with common chemical defenses, univoltinism, larval ballooning, and overwintering as eggs or larvae (Barbosa et al., 1989). Clearly neither these nor the cold hypothesis provides a general explanation for sexual wing dimorphism, but all three point out the complex connections between such dimorphism and life-history traits.

Roff and Fairbairn (1991) found reproductive advantages of brachyptery for females, but not males. This inequality may, in fact, be one factor behind the relative commonness of +W♂/−W♀ species. Evolution of such dimorphism would, of course, depend on preexistence of a suitably modifiable genetic control system. Given that sex determination is usually chromosomal, it seems possible that a locus on one of the sex chromosomes might modify the effects of a somatic allele for brachyptery to produce various kinds of sex-linked patterns of dimorphism.

How does Omalium flavidum *fit in?* Omalium flavidum is one of the few insect species known to have ±W males and −W females, and is the first such species recorded in the large and biologically diverse beetle family Staphylinidae.

Omalium flavidum is unusual among wing-dimorphic beetle species in exhibiting dimorphism of two wing-associated abdominal structures (palisade fringe and tergal wing-folding patches). Hammond (1979, 1985) found only a few cases of variability in one or both of these structures in wing-dimorphic beetle species; in those cases, the +W morph retained and the −W morph lacked the structure in question. *Glypholoma rotundulum,* mentioned above, has reduced wing-folding patches in the micropterous morph (see below). In *O. flavidum,* the loss of wing-folding patches is fully correlated with wing loss, but the palisade fringe is lost only in females (see Table 1). The tergite 3 groove usually present in winged (but not wingless) species of Omaliini is vestigial in females and both male morphs.

The patterns of variation found in *O. flavidum* differ from the other cases of wing-variation known so far in Omaliinae in being sexually dimorphic and apparently geographically undifferentiated. *Glypholoma rotundulum* was described (Thayer and Newton, 1979) from southeastern Australia on the basis of over 200 micropterous (there called "brachypterous") males and females from several sites, plus 2 truly brachypterous individuals (1 ♂, 1 ♀) and 1 macropterous ♂ from the two (very close) northernmost sites. Based on the type series and additional material I have seen (including macropterous males and females from the same and two additional localities; Thayer, unpublished), tests like those in Table 3 support the hypothesis that fully-winged individuals occur at the same (low) frequency in both sexes of *G. rotundulum.* The abdominal wing-folding patches are dimorphic in this species, being larger in macropters and brachypters than in micropters. Brachypterous and macropterous individuals of this species are still known only from the northernmost localities for the species and the micropterous form, universal elsewhere, has not been collected at those sites. Hammond (1985) mentioned wing dimorphism in four other species of Omaliinae, none of which appears to be sexually wing-dimorphic. Three of these (*Olophrum fuscum* (Gravenhorst), *Eucnecosum* (as *Arpedium*) *brachypterum* (Gravenhorst), and *Acidota cruentata* Mannerheim), with macropters rare to very rare,

have the wing-folding patches monomorphic and smaller than those of related macropterous species. The fourth, *Anthobium unicolor,* has varying frequencies of macropters over its range; Hammond did not discuss its wing-associated structures.

There is also a slightly odd pattern of abdominal spiracle size in *O. flavidum.* All morphs have the spiracles of segment 1 larger than those of segments 2 and 3, which are in turn larger than those of segment 4; this seems to be the normal configuration in at least Omaliini (Thayer, unpublished) and probably a much wider group. The spiracles on segments 1–3 of macropterous males are larger than the corresponding ones of −W males (Figs. 4, 6, 21 vs. 5, 7, 22). Winged species of Omaliini similarly have larger spiracles 1–3 than do wingless species, and such a difference has also been found between +W and −W species in Chrysomelidae (Rüschkamp, 1927) and Dytiscidae (Jackson, 1956). The (−W) females of *O. flavidum* also have larger spiracles than −W♂, however. This could reflect higher oxygen needs of egg production compared to sperm production, or perhaps greater locomotory activity among females than −W males. I have not seen a sex-based difference in spiracle size in wingless species of Omaliini, and neither Rüschkamp (1927) nor Jackson (1956) mentioned any differences between the sexes in this regard. Divergence in spiracle size may be greatly underreported, however, since (like wing-muscle development) it is not a character usually examined in taxonomic work.

As discussed earlier, wing dimorphism has been shown to be variously genetically or environmentally controlled (or a combination) in different species. From the limited data available, it appears that in Coleoptera (as in other Holometabola) it is usually genetically determined (Roff, 1986a). In the absence of any rearing data or evidence regarding seasonal change in morph frequencies, it is impossible to say how wing dimorphism is determined in *O. flavidum.* If there are indeed no +W females, the mechanism in this species is clearly not a simple single-locus, two-allele, autosomal genetic system with brachyptery dominant, like that found in several species of Coleoptera (Carabidae, Curculionidae) and Diptera (Sphaeroceridae) cited by Roff (1986a). Two possibilities are: (1) some form of direct genetic sex-linkage or (2) sex-determined effects on hormonal mediation of wing development, with females reacting in one way and males in either of two ways.

Most previously reported ±W♂/−W♀ species have male morphs that are at least partly sympatric (Dermestidae: *Thylodrias contractus,* Barber, 1947; Sciaridae [Diptera]: *Pnyxia scabiei,* Hackman, 1964; some Embioptera, CSIRO, 1970; but not Tipulidae [Diptera]: *Pedicia hannai,* Hackman, 1964; Byers, 1969). Not all known *O. flavidum* localities are represented by specimens of all morphs (or even both sexes), but both male wing morphs are widely distributed over the range of the species; no clinal variation in occurrence vs. latitude is evident (Fig. 1), in contrast to numerous species mentioned by Roff (1990b). There is no other obvious pattern of geographical restriction, and the two male wing morphs have been collected together at four sites so far; *O. flavidum* is thus not unusual among ±W♂/−W♀ species in the geographical distribution of its male morphs.

The driving force favoring evolution of wing dimorphism in *Omalium flavidum* (or brachyptery, if its dimorphism is a transitional stage) is not yet clear, perhaps in part because of the limited ecological data available. As mentioned above, the species inhabits the widespread eastern North American deciduous and deciduous-coniferous forests. Before the widespread forest clearing that accompanied European settlement,

this climax forest biome had a far more continuous distribution than it does now. This would have provided large areas of relatively unbroken favorable habitat for *O. flavidum,* presumably with scattered areas of disturbance caused by severe storms or occasional treefalls. Several authors (Southwood, 1962; Harrison, 1980; Hammond, 1985; Roff, 1986a) have suggested that conditions such as these favor evolution (in both sexes) of either wing-dimorphism or brachyptery, depending on the level of habitat stability. Could bisexual dimorphism be a stage that *Omalium flavidum* has already passed through, en route to brachyptery? Such a pathway to brachyptery can be envisioned: under conditions allowing brachyptery, if the energy conservation hypothesis is valid, stronger (hence faster) selection for wing loss in females than males might occur because of the greater reproductive investment by females than males. If this were the case, however, one would expect wing dimorphisms like that of *O. flavidum* to be far more common.

On an ecological time scale, the eastern forests have constituted a relatively stable habitat for a long time; their stability, however, does not extend very far back on a geological scale. All but the southernmost records of *O. flavidum* (southern Pennsylvania, District of Columbia vicinity) are from areas that were ice-covered during the Pleistocene glaciations (Fig. 1; Flint, 1971; Morgan and Morgan, 1981). Thus, the eastern forests only came to occupy a large part of the present range of *O. flavidum* during the last 8,000–10,000 years (Matthews, 1979), presumably moving in from the south (and/or east, if the continental shelf formed a glacial refugium; Flint, 1971). Obviously, stable forest did not appear immediately behind the disappearing glaciers, so the time available for colonization by mature-forest inhabitants such as *O. flavidum* would have been even less.

When did wing loss develop in *O. flavidum*? Three alternatives can be proposed if the wing loss is assumed to be a result of habitat stability. First, if wing loss developed independently in many newly established local populations as a result of relatively stable habitats, one would expect to find a distribution pattern like that of *Calathus mollis* (Carabidae) in Scandinavia (Lindroth, 1979), with brachypterous forms predominating in the longest-occupied (southern) areas. No such pattern is apparent in the data available for *O. flavidum,* so this appears not to be the explanation. Second, if dimorphism arose only after *O. flavidum* had fully occupied more or less its present range, the phenomenon would not necessarily occur throughout the species' range, and morph frequencies might be expected to vary more or less randomly over space. Multiple population samples (taken throughout the year) would be needed to test this hypothesis; the data now available for *O. flavidum* are far too scanty for such purposes. Finally, the species might already have had its present form of wing-dimorphism while in a glacial refugium and when the ice sheet began to retreat, managed to disperse over a large area despite the flightlessness of females. Although this seems absurd at first glance, over a period of 8,000 years it would require movement on the order of 100 m per year, which might be possible. (Morgan and Morgan, 1981, arrived at a similar conclusion for a flightless species of Carabidae.)

Alternatively, *O. flavidum*'s seasonal pattern of occurrence, seeming to reflect a preference for (adaptation to?) cool to cold conditions, and the (partly) sexual nature of its dimorphism, suggest that wing-dimorphism in this species might be an example of a cold-adaptation pattern such as discussed above (Downes, 1965; Byers, 1969).

Further knowledge of the distribution and seasonality of the species, study of larger samples of multiple populations, investigation of the genetic basis of its wing dimorphism, and more detailed information about its habits and microhabitat may help to clarify the factors involved in the evolution of the unusual wing dimorphism found in *Omalium flavidum*. Understanding this case might also help to elucidate the reasons for the evolution of a similar pattern in other taxa and for the rarity of this pattern.

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APPENDIX A

Redescription of "*Omalium*" *flavidum* Hamilton
and Lectotype Designation

Redescription. Yellowish- or reddish-brown to dark brown, varying among morphs (see Table 1). Body sparsely punctate and sparsely setose (Figs. 4, 5); dorsal surfaces of head (except neck), pronotum, and elytra without microsculpture; abdomen with reticulate microsculpture of varying distinctness.

Head (Figs. 8, 9) with pair of ocelli on vertex, often concolorous with surrounding cuticle (thus difficult to see); head width 1.2–1.3 × head length; distinct neck present; frontal area elevated, delimited posteriorly by oblique ridges running from behind antennal bases to just in front of ocelli; eyes well-developed (somewhat reduced in −W♂ and ♀), with seta-fringed ridge posterior to each eye (Figs. 8, 9); cuticle above and behind eye with curved ridges roughly paralleling margin of eye; gular sutures close but not confluent between eyes, diverging posteriorly. Labral apex arcuately emarginate; epipharynx with sensilla and setae arranged as in Figure 14. Mandibles apically acute, asymmetrical, each with well-developed articulated mola bearing vertical ridges on adoral surface; ventral surface of each mandible near middle with band of mostly apically bifid setae running from anterolateral to posteromedial; right mandible with a single sharp preapical tooth, left with a blade-like preapical area. Galea (Fig. 13) with densely setose apex; lacinia with medial comb of spine-like setae and unarticulated apical spine (Fig. 13); maxillary palp with 4 articles, all but first subequal in maximum width, ultimate about 2.5 × as long as penultimate (Figs. 8, 9). Labial palp of 3 articles subequal in width, the ultimate longest, penultimate shortest. Antenna 11-segmented, without distinct club, longer than head and pronotum together (length varying among morphs: see Tables 1, 2); with dense long blunt sensilla on antennomeres 3–11 in ♂, 5–11 only (and concentrated at apices) in ♀; +W♂ with all antennomeres longer than wide, ♀ and −W♂ with antennomeres 1–3 and 11 longer than wide, 6–10 wider than long, and 4–5 quadrate or slightly wider than long; antennomere 3 slightly wider in −W♂ than in ♀.

Pronotum (Figs. 4, 5) slightly transverse, width about 1.25 × length, widest slightly anterior to middle, narrowed slightly sinuately from there toward base; lateral margins narrowly explanate; disc with raised roughly triangular median area enclosing longitudinal impressions on either side of midline.

Elytra of +W♂ loosely interlocked, with arcuate apices, length about 1.5 times conjoint width and nearly 3 times as long as pronotum, covering part or all of abdominal tergite 5, humeri prominent; of ♀ and −W♂ very tightly interlocked (though not fused), with truncate apices, about as long as their conjoint width and about 1.5 times as long as pronotum, only covering tergite 3, humeri reduced and rounded. Mesosternum not carinate. Metathorax of +W♂ (Fig. 6) normal in size (Fig. 2a, Table 1) and sclerotization, normal flight muscles present, metendosternite as in Figure
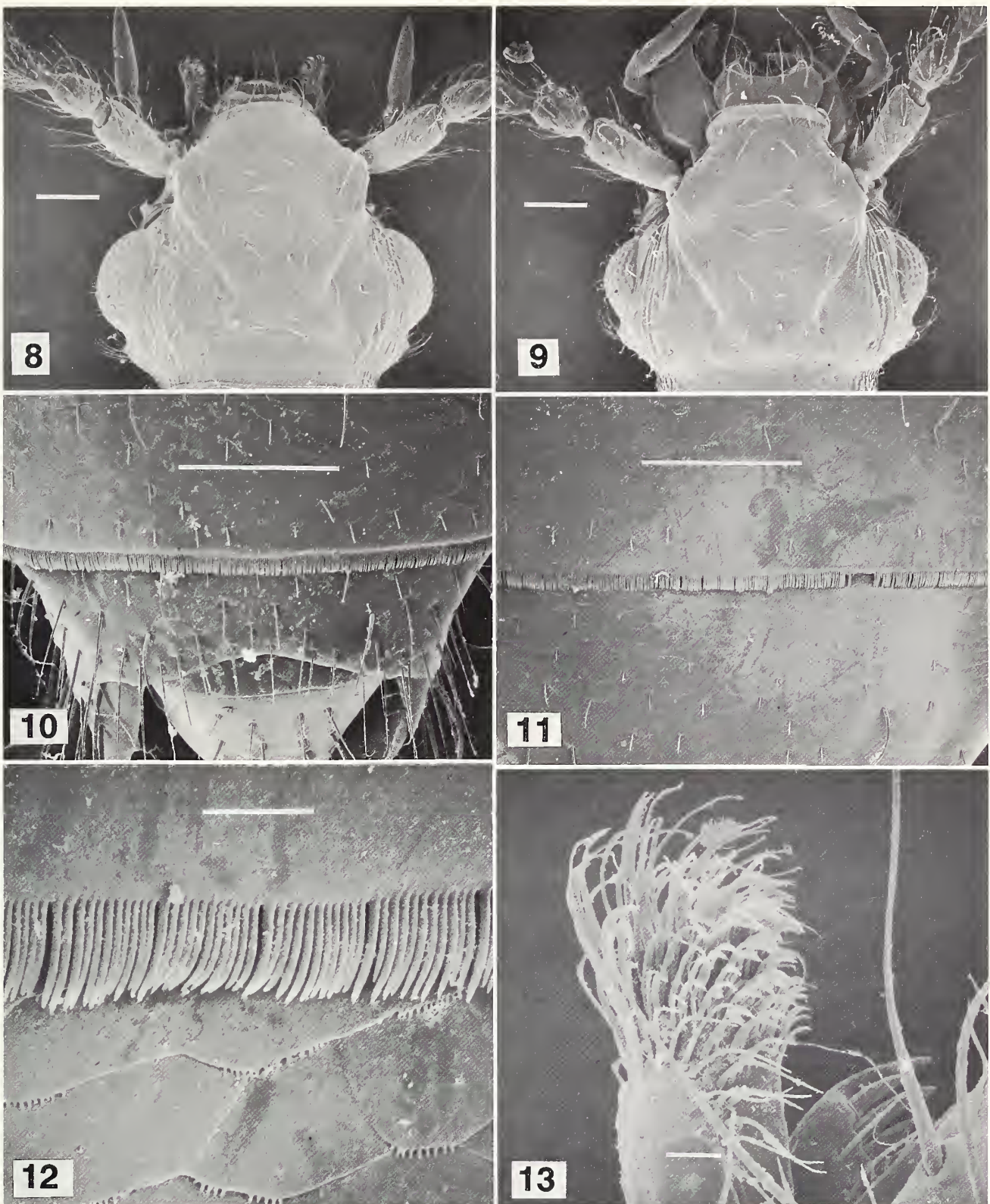
Figs. 8–13. *Omalium flavidum* Hamilton. 8. Head, dorsal view, +W♂. 9. Same, −W♂. 10. Median area of abdominal tergite 7 apex, +W♂. 11. Same, −W♂. 12. Detail of 11. 13. Apex of left galea, +W♂, dorsal view. (Scale line: Figs. 8–11, 100 μm; Figs. 12–13, 10 μm.)

15a; metathorax of ♀ and −W♂ (Fig. 7) reduced in length (Fig. 2a, Table 1), width, and dorsal sclerotization, without flight muscles, metendosternite as in Figure 15b. Wings normally developed (+W♂, Fig. 16a) or minute (♀, −W♂, Fig. 16b).

Tarsi 5-segmented; empodium bisetose, one seta much longer than other (Fig. 19);
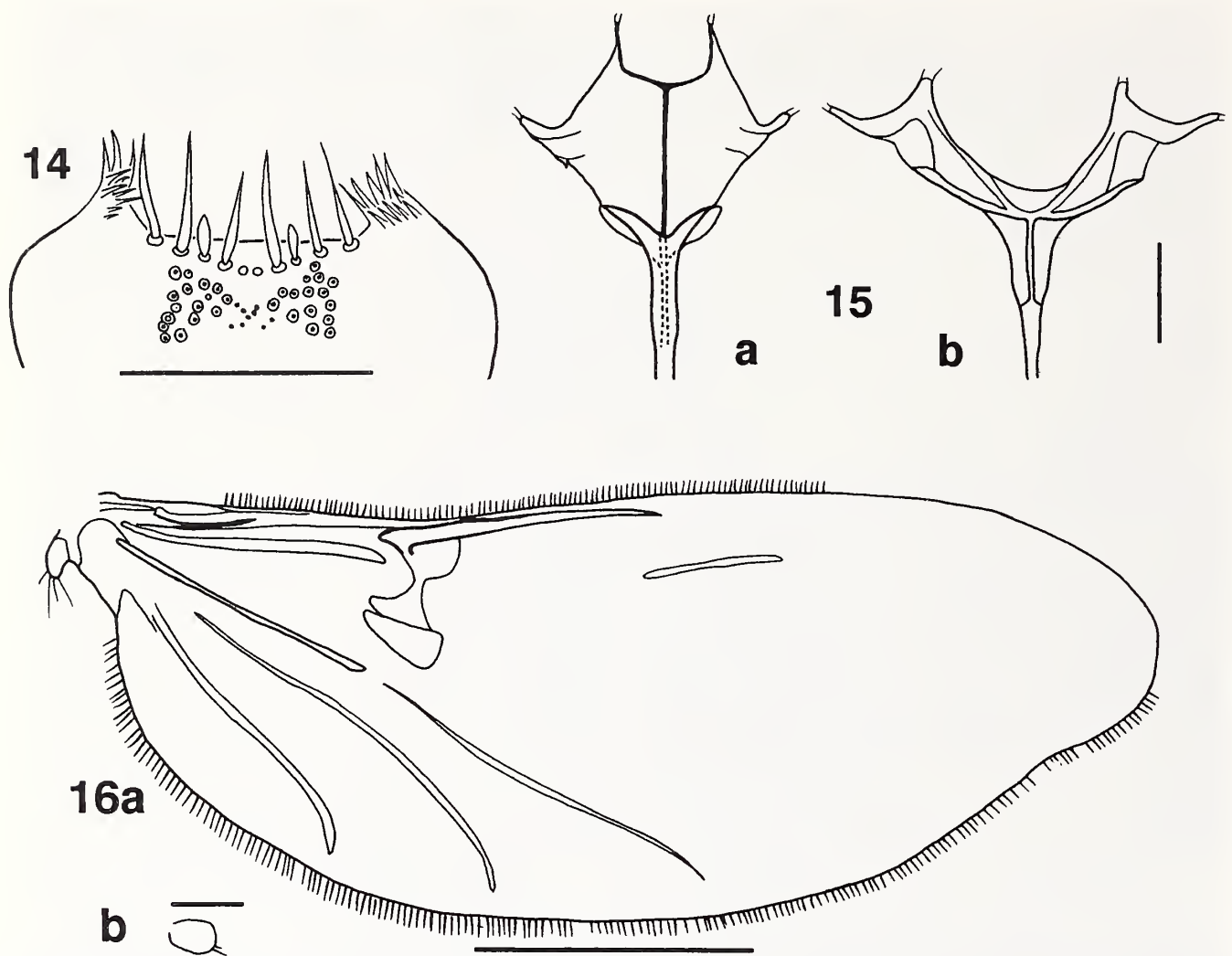
Figs. 14–16. *Omalium flavidum* Hamilton. Scale lines = 0.1 mm, except in Fig. 16a, 1 mm. 14. Epipharynx, ♀, ventral view. 15. Metendosternite, dorsal view. (a) + W♂; (b) −W♂. Right wing, dorsal view. (a) +W♂; (b) −W♂.

+W♂ with hind tarsus (Figs. 2b, 17) about two-thirds as long as hind tibia, tarsomeres 1–4 together longer than 5 (Fig. 2c, Table 1), ♀ and −W♂ with hind tarsus (Figs. 2b, 18) no more than 0.6 as long as hind tibia, tarsomeres 1–4 together shorter than 5 (Fig. 2c, Table 1).

Abdomen with spiracles on segments 1–8, located in tergite of segments 3–7, in membrane adjacent to tergite of segments 1–2 and 8; spiracles 1–3 distinctly (♀, +W♂) or slightly (−W♂) larger than following ones; one pair of paratergites on each of segments 3–7; intersegmental membranes connecting segments 3–7 bearing brick-

→

Figs. 17–20. *Omalium flavidum* Hamilton, tarsi. 17. Hind tarsus, +W♂, dorsal view. 18. Same, −W♂, oblique ventral view. 19. Detail of 18, showing unequal empodial setae. 20. Front tarsus, −W♂, dorsal view. (Scale line: Figs. 17–18, 20, 100 μm; Fig. 19, 25 μm.)

Figs. 21–24. *Omalium flavidum* Hamilton, abdominal tergites. 21. Tergite 3, with arrow indicating vestigial row of setae near apex, +W♂. 22. Same, −W♂. 23. Tergites 4 and 5, +W♂. 24. Same, −W♂. (Scale line: Figs. 21–22, 100 μm; Figs. 23–24, 200 μm.)
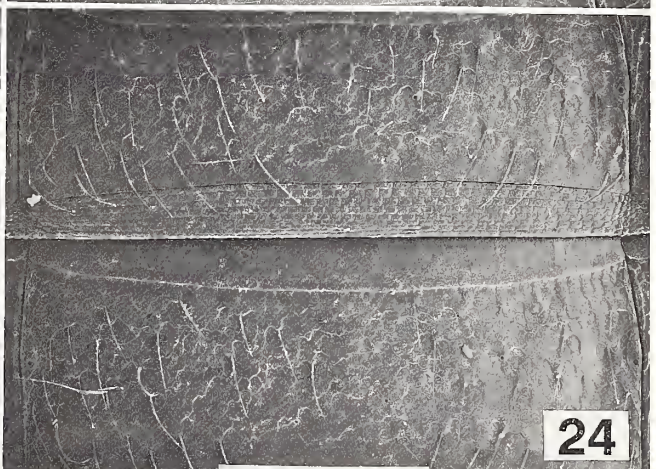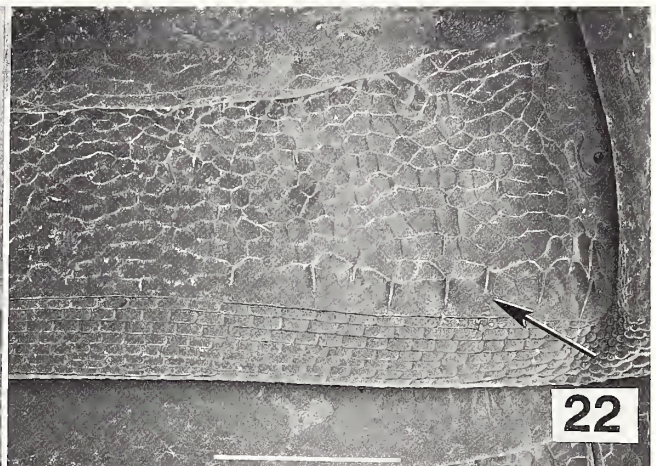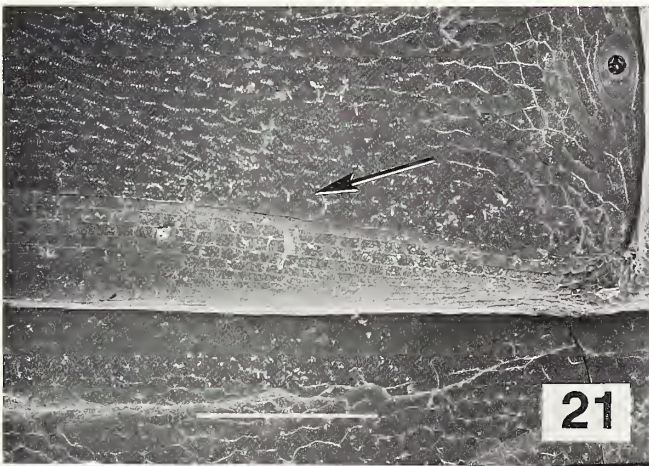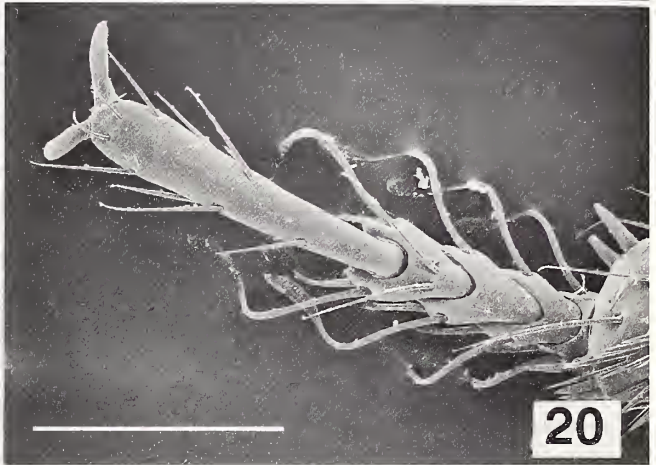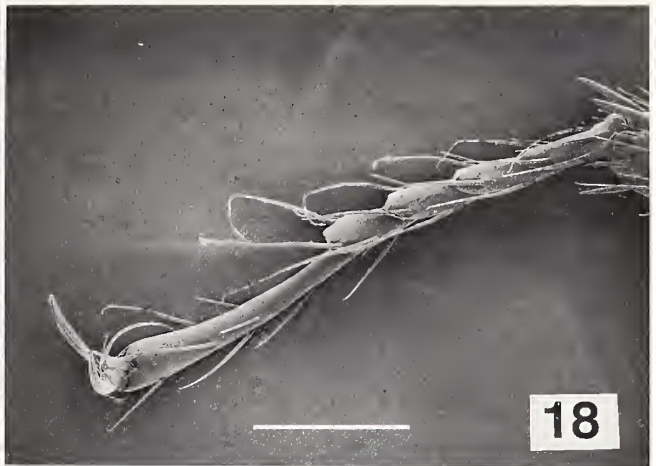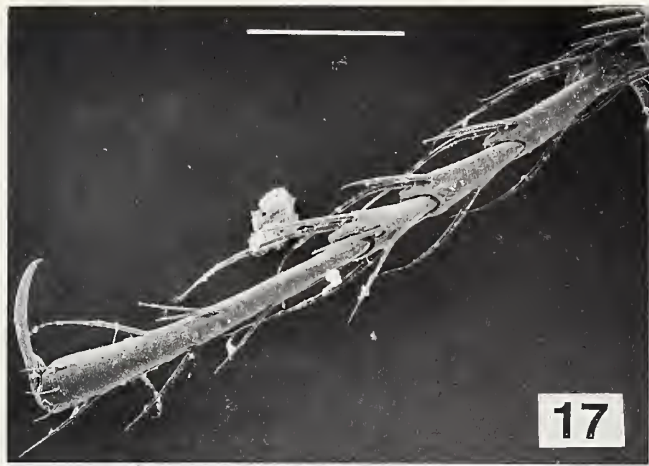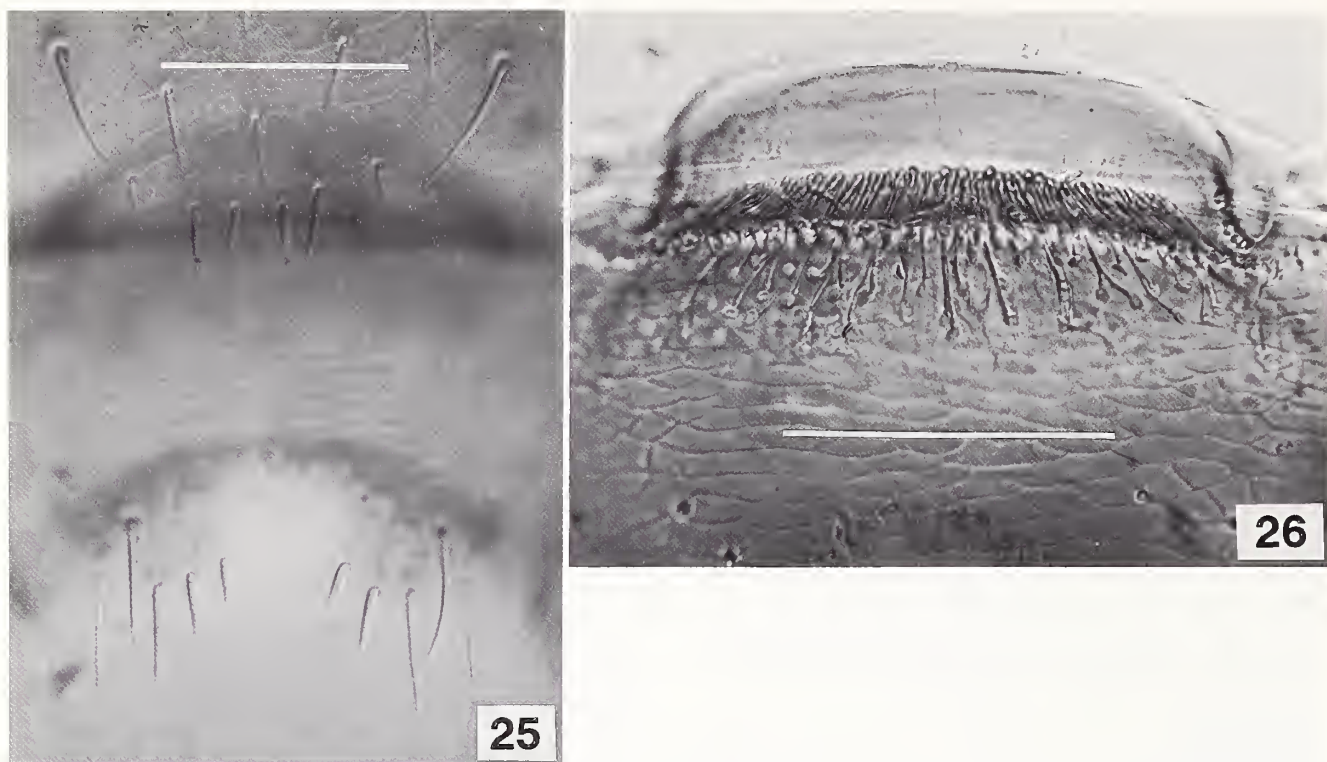
Figs. 25, 26. *Omalium flavidum* Hamilton, abdominal sternites. 25. Sternites 7 and 8, −W♂, ventral view. 26. Anterior median projection of sternite 8 with associated gland tubules, +W♂, ventral view. (Scale line: 0.1 mm.)

wall pattern of sclerites (Figs. 21–24); tergite 3 posteriorly with vestiges of transverse seta-edged groove (Figs. 21, 22); sternite 3 with distinct hind coxal impressions delimited by a ridge; wing-folding patches present on tergites 4–5 of +W♂ only (Fig. 24, cf. Fig. 23); tergite 7 with (±W♂, Figs. 10–12) or without (♀) apical palisade fringe; sternite 8 with anterior projection bearing ducts of defensive gland cells (Fig. 26).

Male. Front tarsus with tenent setae on tarsomeres 1–4 (Fig. 20). Sternites 7 and 8 with characteristic arrangement of short stout setae apically (Fig. 25); genital segment (Fig. 27) with tergite 9 continuous across dorsum. Parameres of aedeagus dorsal when aedeagus is retracted within abdomen; aedeagus as in Fig. 28, with small thin basal piece, median lobe with median desclerotized band at base and on abparameral side, and internal sac with complex armature of small spines and sclerotized plates.

Female. External genitalia (Fig. 29) lacking sternite 9; tergite 9 divided dorsally; tergite 10, two pairs of gonocoxites, and one pair of styli present; lightly sclerotized structure present internally, extending anteriorly from tergites 9 and 10 when genitalia are extended, including a flat portion in median sagittal plane and small pale oval "window" in horizontal plane on each side of it, near anterior end (Fig. 29, broken lines). Spermatheca (Fig. 30) lightly sclerotized, two-chambered.

Lectotype designation. Hamilton (1896) stated that "several examples occurred near St. Vincent." His collection is at the Carnegie Museum, which houses two apparent syntypes of *O. flavidum*. I here designate as lectotype the intact female, bearing the labels: St. Vinc. Penn./type/Carn. Mus. Acc. 349/[blank red label]/LECTOTYPE Omalium flavidum Hamilton des. M. K. Thayer 1991. I designate the male (−W morph, abdomen missing) a paralectotype; its labels read: St. Vinc. Penn./Carn. Mus. Acc. 349/PARALECTOTYPE Omalium flavidum Hamilton des. M. K. Thayer 1991.

APPENDIX B

Material Examined (all ♀ are −W)

Canada: ONTARIO: 2♂ (−W), 3♀, Chaffeys Locks, birch-maple litter beside logs, 23.x.1985 (A. Davies) (CNC); 1♂ (+W), Kemptville, intercept, 25.x–8.xi.1983 (L. Dumouchel and J. Denis) (CNC); QUÉBEC: 1♂ (−W), Johnville, TP-066, 4.v.1988 (C. Levesque) (CNC). **United States:** DISTRICT OF COLUMBIA: [no locality], 1♂ (−W) (CM); MAINE: Androscoggin Co.: 1♂ (+W), Poland Spring, 27.xi.1909 (JHE) (MCZ); York Co.: 5 ♂ (+W), West Lebanon, 20–29.xi.90, FIT, disturbed forest (DW Barry) (UNH); 3♂ (+W), West Lebanon, FIT, disturbed forest, 30.xi–5.xii.90 (DW Barry) (UNH); 20♂ (+W), West Lebanon, FIT, disturbed forest, 11–17.xii.90 (DW Barry) (UNH); 16♂ (+W), West Lebanon, FIT, disturbed forest, 18–26.xii.90 (DW Barry) (UNH); 1♂ (+W), West Lebanon, FIT, disturbed forest, 27.xii.90–7.i.91 (DW Barry) (UNH); 2♂ (+W), West Lebanon, FIT, disturbed forest, 6–12.ii.91 (DW Barry) (UNH); 2♂ (+W), West Lebanon, FIT, disturbed forest, 15–24.iii.91 (DW Barry) (UNH); 1♂ (+W), West Lebanon, FIT, disturbed forest, 25–31.iii.91 (DW Barry) (UNH); MARYLAND: Prince Georges Co.: 1♂ (+W), Takoma Pk., 3 mi E, flying, 17.xii.1949 (G. H. Nelson) (GHN); MASSACHUSETTS: Hampshire Co.: 1♂ (−W), Northampton, 14.xi.1917 (CNC); Middlesex Co.: 1♀, Framingham, sifting, 17.xi.1934 (C. A. Frost) (MCZ); 3♂ (2 +W, 1 −W), 1♀, Tyngsboro, 17.xi.1901 (MCZ); 1♀, Tyngsboro, 3.xi.1915 (MCZ); 1♂ (−W), Tyngsboro, sifting leaves, 7.xi.1924 (MCZ); NEW HAMPSHIRE: Carroll Co.: 3♂ (−W), 1♀, Passaconaway Cpgd., spruce-fir-pine-hdwd., 340 m, leaf and rain-washed litter, berl., 17–18.x.1973 (A. Newton) (ANMT); 1♀, Passaconaway Cpgd., spruce-fir-pine-hdwd., 340 m, leaf and rain-washed litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); 1♂ (+W), The Bowl, 2.5 mi NW Wonalancet, 590 m, FIT, 20.x–7.xi.1984 (D. S. Chandler) (UNH); 1♂ (−W), The Bowl, 2.5 mi NW Wonalancet, 590 m, sift birch log, 1.xi.1984 (D.S. Chandler) (CNC); 1♀, The Bowl, 2.5 mi NW Wonalancet, 590 m, sift conifer logs, 17.x.1985 (D. S. Chandler) (UNH); 1♂ (−W), The Bowl, 2.5 mi NW Wonalancet, 590 m, sift birch logs, 31.x.1985 (D. S. Chandler) (UNH); 30♂ (28 +W, 2 −W), The Bowl, 2.5 mi NW Wonalancet, 590 m, FIT, 1–19.xi.1985 (D. S. Chandler) (UNH); 3♂ (2 +W, 1 −W), The Bowl, 2.5 mi NW Wonalancet, 590 m, on snow, 19.xi.1985 (D. S. Chandler) (UNH; CNC); Coos Co.: 1♂ (−W), Mt. Washington toll rd, 0.3 mi below Halfway Hse., spruce-fir-birch for., 1100 m, litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); Grafton Co.: 1♀, Franconia, 26.xii.1960 (K. W. Cooper) (USNM); 1♀, Hubbard Brook Exp. For., Bear Brook, 460 m, sift rotten wood, 15.x.1982 (D. S. Chandler) (UNH); 3♂ (−W), 3♀, Kancamagus Pass, spruce-fir-birch, 850 m, litter, berl., 19.x.1973 (A. Newton) (ANMT); 1♀, Kancamagus Pass, spruce-fir-birch, 850 m, litter, berl., 15.x.1978 (A. Newton and M. Thayer) (ANMT); Strafford Co.: 5♂ (+W), Durham, 1 mi SW, FIT, 15.x–4.xi.1987 (D. S. Chandler) (UNH); 2♂ (1 +W, 1 −W), Durham, 1 mi SW, FIT, 18.xi–4.xii.1987 (D. S. Chandler) (UNH); 15♂ (14 +W, 1 −W), Spruce Hole, 3 mi SW Durham, FIT, 5–24.xi.1987 (D. S. Chandler) (UNH; CNC); 6♂ (+W), Spruce Hole, 3 mi SW Durham, FIT, 4–15.xii.1987 (D. S. Chandler) (UNH); NEW YORK: St. Lawrence Co.: 1♀, Wanakena [as Wananeka], 15.x.1982 (Lee Herman) (AMNH); Tompkins Co.: 1♂ (+W), Caroline, on snow, 12.iii.1963 (M. A. Deyrup) (AMNH); 1♂ (+W), Ithaca, 10.iv.1926 (Fletsher) (CU); 1♀, Jacksonville, N, maple+ forest, dead maple buttress, FMHD #82-49, 24.v.1982 (W. S. Suter) (FMNH); PENNSYLVANIA: 1♀, [state only] (CM); Philadelphia Co.:

27a   b   28a

29a   b   b   30
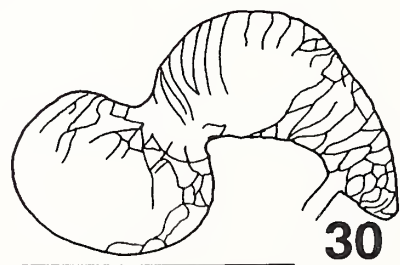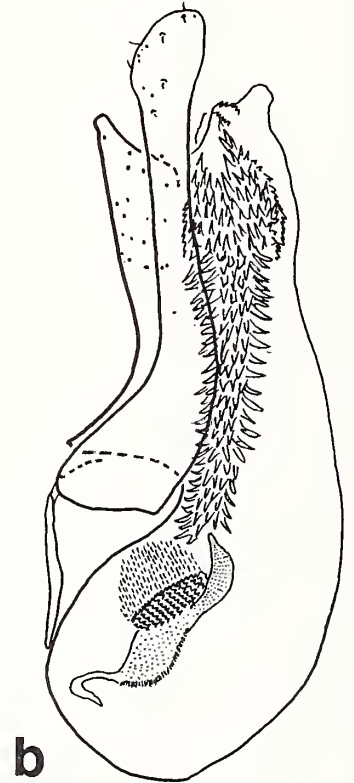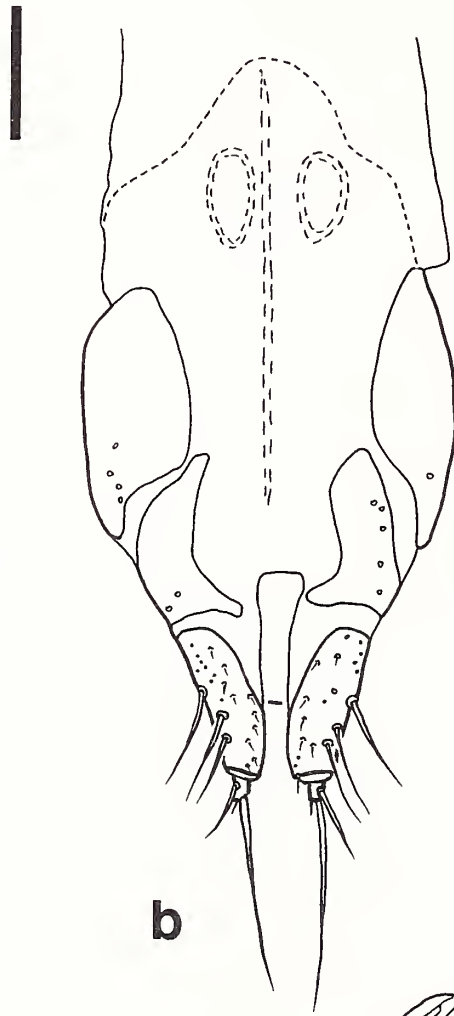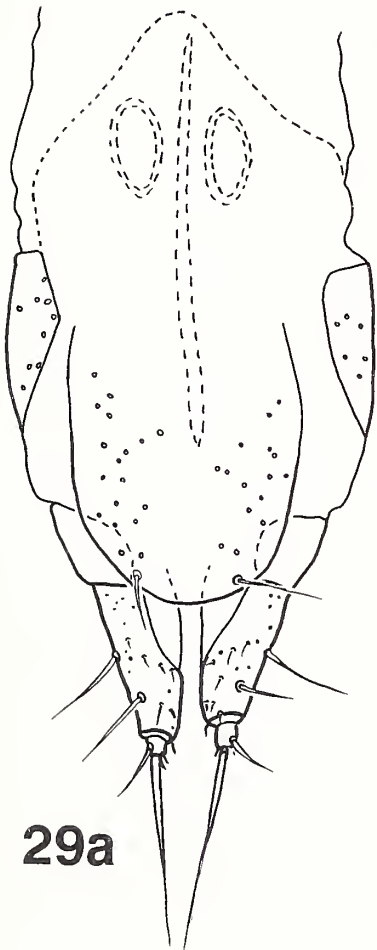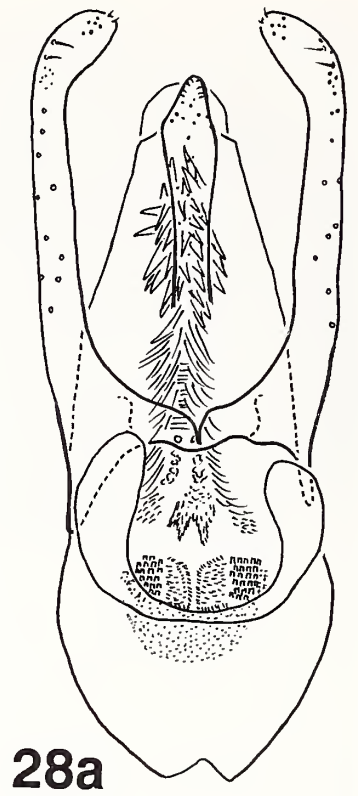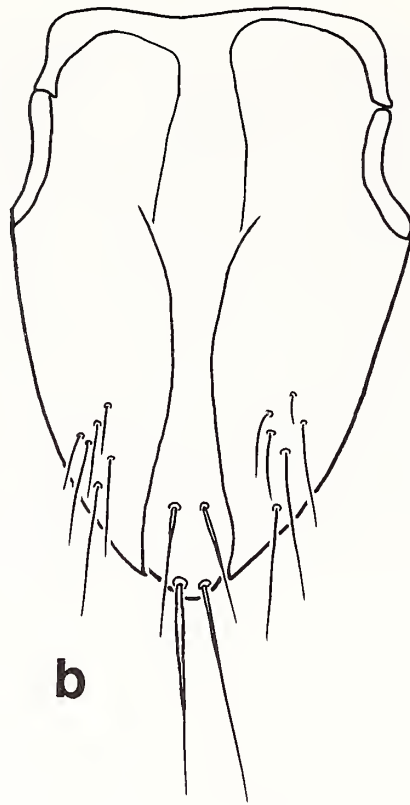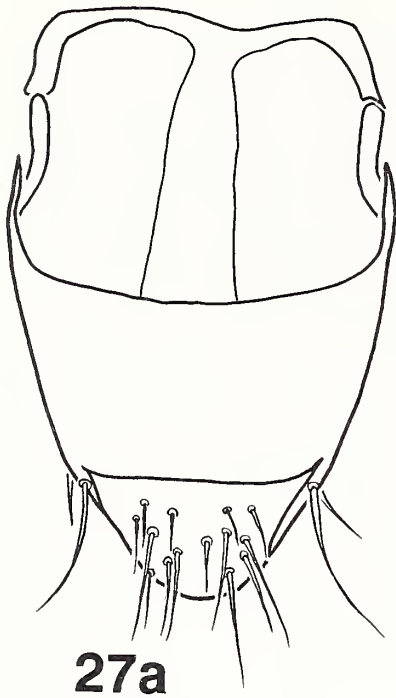
1♂ (−W), Manayunk [as Manyunk], 5.x (J. W. Green colln.) (CAS); Schuylkill Co.: 1♂ (+W), Pottsville, forest, trap #203, 1–11.iv.1967 (S. Peck) (FMNH); Westmoreland Co.: 1♀, Jeannette, x (H. G. Klages) (CM); 1♀, Jeannette, xii (H. G. Klages) (CM); 1♀, Jeannette, "VIII.16" (H. G. Klages) (CM); 1♂ (+W), Powdermill Nature Res., nr Rector, cabins area on snow, 25.ii.1958 (CM; CM Acc. 18464); 1♂ (−W) (Paralectotype), 1♀ (Lectotype), St. Vincent [as St. Vinc.] (CM).

←

Figs. 27–30. *Omalium flavidum* Hamilton. Scale lines = 0.1 mm. 27. Male genital segment (segments 9–10), +W. (a) dorsal view; (b) ventral view. 28. Aedeagus. (a) −W♂, parameral view (dorsal in repose); (b) +W♂, lateral view. 29. Female external genitalia, anterior broken lines indicating lightly sclerotized internal sclerite. (a) dorsal view; (b) ventral view. 30. Spermatheca (spermathecal gland attached to subapical duct not shown).